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A TAXONOMIC REVISION OF *LESCURAEA* (INCLUDING *PSEUDOLESKEA*) AND *RIGODIADELPHUS* (LESKEACEAE, BRYOPSIDA) IN NORTH AMERICA

by

Martina Ursula Krieger ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Master of Science

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled A Taxonomic Revision of *Lescuraea* (including *Pseudoleskea*) and *Rigodiadelphus* (Leskeaceae, Bryopsida) in North America submitted by Martina Ursula Krieger in partial fulfillment of the requirements for the degree of Master of Science

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Abstract

A taxonomic revision of *Lescuraea* Bruch & Schimp. *in* B.S.G. (including *Pseudoleskea* Bruch & Schimp. *in* B.S.G) identifies seven species in North America, with infraspecific variation encompassed by six described varieties. New synonymy is proposed for *Lescuraea radicosa* var. *pallida*, synonymy of *L. julacea* with *L. saxicola* by Noguchi *et al*. (1991) is conferred, *Pseudoleskea arizonae* is reassigned to *Pseudoleskeella*, the new combination *Rigodiadelphus baileyi* is presented, and conservation of *Lescuraea radicosa* is suggested. An infrageneric classification of *Lescuraea* is proposed, with subgenera *Lescuraea* and *Pseudoleskea* accommodating one and six species, respectively. Eleven taxa examined from outside North America are removed from *Lescuraea*. A revision of an additional 16 taxa would complete a monograph of *Lescuraea*. A species phylogeny of all accepted taxa in *Lescuraea* is warranted. The phytogeography of the Holarctic genus *Lescuraea* is examined, with the greatest centres of diversity for species of *Lescuraea* being in North America and in Europe.

For my parents Heinz und Ursula Krieger,
my brother Christian and grandmother Hilde Wolfram,
and my beloved Thorsten Hebben

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Chapter 1

INTRODUCTION

Taxonomy is the science of naming, describing, identifying, and classifying organisms based on morphology (Bischler and Boisselier-Dubayle 1998) and other aspects of organismal biology, thus potentially reflecting patterns of relationships (Novacek 1992). This field has been pursued by both amateurs and researchers alike for at least several hundred years. Although not scientifically accredited, the Bible recounts how Adam named and described organisms around him, making his world more orderly. In the mid 18th century, Carolus Linnaeus was likely the most prominent living taxonomist. In the discipline of Bryology, Johannes Hedwig named and described a myriad of species by 1801. He was able to sort taxa into natural and understandable genera, many of which are still in use today. Consequently, Hedwig came to be known as the father of moss taxonomy, with the starting point of nomenclature for Musci (the Sphagnaceae excepted) coinciding with Hedwig's (1801) publication 'Species Muscorum.' In the late 1930's, genetic and ecological dimensions were added to what was then an exclusive morphologically based taxonomy (Hawksworth and Bisby 1988).

Taxonomy is by definition, a methodical science that attempts to organise nature. It is both practical in producing an understandable arrangement of species into genera and families, as well as potentially producing a stable and useful nomenclature (Crum 1991). Unfortunately, nature is somewhat disorderly. According to Crum (1991) a species has

> ecological requirements and occupies a range reflective of its origin and migrational histories. It is a product of genetic and evolutionary change, and it continues to vary and adapt to its environment. It is concerned with ecology, physiology, and morphology, and those disciplines and others contribute to the evolutionary schemes of classification.

Despite the disorder associated with organisms, these factors certainly do not make taxonomy an effortless or insignificant science. However, Hawksworth and Bisby (1988) indicated "taxonomic studies have come to occupy a place of decreasing importance in biology, which has led to an even greater decline in the training of taxonomists." Unfortunately, the importance of understanding the taxonomy of organisms is often overlooked. Knowledge of species, including their biogeographical and historical distributions, is fundamental to discussions of conservation priorities (Stiassny 1992). Furthermore, interest in the use of organisms as monitors of environmental change and contamination has also increased dramatically (Hawksworth and Bisby 1988), requiring a thorough understanding of species themselves. Frequently, taxa "escape question as they come to be sanctioned by usage and hallowed by tradition, but they need, over and again, to be re-evaluated" (Crum 1991). Thus, taxonomy may be regarded as "the operational core of systematics" (Novacek 1992).

Systematics, which is the aspect of science that deals with the organisation, history, and evolution of life, ultimately asks the following questions: "How did life forms originate? How did they diversify, and how are they distributed both in space and time" (Novacek 1992)? In order to answer these questions, the taxonomy of taxa must be understood comprehensively. Although the circumscription and ranking of taxa is subjective, dependent on the knowledge and 'intuition' of the researcher, it is nevertheless an important task. Consequently, the circumscription and classification of taxa is often not complete, but changes when research identifies a problem within a group.

According to Crum (1991), mosses present somewhat unusual problems in taxonomic and phylogenetic interpretation since both gametophytes and sporophytes are available for analysis. Gametophytes are more elaborately differentiated than sporophytes, and as such present "greater degrees of resemblance and difference and are more useful in sorting out species." On the other hand, "the sporophyte is a relatively stable structure that is often useful in separating out higher taxonomic categories" (Crum 1991). Research has shown that the gametophyte exhibits a great deal of variation at the species level owing to environmental variables. However, recent observations (e.g., Vitt 1981, Buck and Vitt 1986, Buck and Crum 1990, Buck 1991) suggest that the "reduction of peristome parts has recurred in the evolution of sporophytes of many families as a response to environmental selection" (Crum 1991). According to Crum (1991), "the peristome is a functional structure, and it is unreasonable to assume that is has not adapted for use and varied accordingly." As a result of peristomial differences associated with reduction series, gametophytically similar taxa have traditionally and continue to be treated either in separate genera (e.g., *Leskeella* and *Pseudoleskeella*) or in a single genus of broad scope.

Some members of the Leskeaceae have long been included in the Thuidiaceae, but they have also been separated from the latter partly due to variously reduced peristomes of several taxa of the group. Buck and Crum (1990) recognised the Leskeaceae "primarily on the basis of gametophytic characters … and perceive[d] a habitat-driven, sporophyte reduction series." In addition, they indicated that peristomial reduction series "are valid markers of lineage at the generic level" (Buck and Crum 1990). Consequently, they treated the following taxa at the generic level: *Leskeella*, *Pseudoleskeella*, *Lescuraea*, and *Pseudoleskea* (for example), and disagreed with their treatment as two genera of broader scope, namely *Pseudoleskeella* (including *Leskeella*) and *Lescuraea* (including *Pseudoleskea*).

The circumscription and classification of taxa may never be absolute, but is amended when research identifies a problem within a group. The generic delimitation of both *Lescuraea* and *Pseudoleskea* has had a long and diverse history, with nine and 31 accepted species respectively, worldwide (Crosby *et al.* 1999). Of these, three and eight taxa are listed for *Lescuraea* and *Pseudoleskea* respectively, in North America (Wijk *et al.* 1964, 1967). The objectives of this study are to revise the North American taxa in *Lescuraea* Bruch & Schimp *in* B.S.G. and *Pseudoleskea* Bruch & Schimp. *in* B.S.G; examine the phytogeographical distribution of taxa; and propose hypotheses of diversification. A reassessment of the enumeration of the North American taxa is made, taxa are grouped, and an infrageneric classification of *Lescuraea* is proposed. In addition, several species found elsewhere are examined and placed in other genera or families.

In the future, revision of additional 16 taxa would complete a monograph of *Lescuraea*. Furthermore, a species phylogeny of all accepted taxa in *Lescuraea* should be established. Hypotheses of infrageneric relationships and a detailed infrageneric classification can then be presented, thus supporting or providing insight into the proposed classification.

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Chapter 2

A SYNOPSIS OF THE MOSS GENUS *LESCURAEA* BRUCH & SCHIMP. *IN* B.S.G. *SENSU LATO* (LESKEACEAE, BRYOPSIDA) IN NORTH AMERICA

2.1. Historical Background of *Lescuraea* Bruch & Schimp. *in* B.S.G. including *Pseudoleskea* Bruch & Schimp. *in* B.S.G.

The genus *Lescuraea*, named after Swiss-American bryologist and paleobotanist, Léo Lesquereux, was first described by Bruch and Schimper (1851), in Bruch *et al.* (1851) Bryologia Europaea II. Bruch and Schimper (1851) included three elements in their generic concept: 1) *Lescuraea striata* (Schwägr.) Bruch & Schimp. *in* B.S.G. (= *Lescuraea mutabilis* Brid. (Hagen)) and 2) *L. striata* var. ß *saxicola* Bruch & Schimp. *in* B.S.G. (= *Lescuraea saxicola* (Bruch & Schimp. *in* B.S.G.) Molendo) from Europe, and 3) the North American species *Leskea rigescens* Wils. *in* B.S.G. (*nomen nudum*), known today as *Lescuraea stenophylla* (Ren. & Card.) Kindb.

Although both Bridel (1801) and Hedwig (1801) gave full descriptions of *Hypnum mutabile* Brid. and *Pterogonium striatum* (= *Lescuraea mutabilis*), respectively, only Bridel (1801) published his new species at that time. Hedwig's *Pterogonium striatum* was published after his death, by Schwägrichen (1811) in his 'Supplements' to Hedwig's (1801) grand publication 'Species Muscorum'. Bruch and Schimper (1851) agreed that Bridel's (1801) name had priority over Hedwig's later published *Pterogonium striatum*. However, they chose to recognise Hedwig's specific epithet.

The North American taxon *Leskea rigescens* was in Drummond's first collection in 1828, and distributed as *Hypnum tenax* no. 225. However, Drummond did not realise that he had a mixed collection. Wilson (1828) discovered that Drummond's collection no. 225 contained two distinct species, one he called *Hypnum congestum* Wils. *ex.* Best (*nomen nudum*) (= *Lescuraea radicosa* (Mitt.) Mönkem.) and the other *Leskea rigescens*. Drummond had used the sterile plants (*Lescuraea radicosa*) to identify his collection as *Hypnum tenax*. However, sporophytes were only present on other plants (*L. stenophylla*). Consequently, he distributed different exsiccates as *Hypnum tenax* no. 225, some of which were *L. radicosa*, and others *L. stenophylla*. Wilson (1828) listed both species in 'Musci Americani: Specimens of the mosses collected in British North America 1, n.

1886, n. 225'. Unfortunately, he failed to describe either new species. Bruch and Schimper (1851) also merely listed both species in Bryologia Europeae II, without providing a description.

Bruch and Schimper (1851) established that a number of authors were hesitant in the placement of taxa. For example, Bridel placed *Lescuraea striata* in *Pterigynandrum*, Schwägrichen combined the species in *Neckera*, and Wilson placed it in the genus *Leskea*. While Bruch and Schimper (1851) wanted to determine the natural genus in which to place *Lescuraea striata* (along with variety ß *saxicola*) and *Leskea rigescens*, they declared that these two species could not be joined with *Pterigynandrum*, or with any other genus with erect capsules. Instead, Bruch and Schimper (1851) commented on the close relationship of these taxa to *Pylaisaea* (= *Pylaisia*). However, placing these species within *Pylaisaea* was also unnatural. These species differed from those in *Pylaisaea* in that they both had stoutly costate leaves, paraphyllia, a weakly hygroscopic and uneven exostome inserted below the mouth of the capsule, an endostome with uneven segments shorter than the exostome teeth, and by the basal membrane being connected to the exostome. As a result, *Lescuraea striata* (with variety ß *saxicola*) and the element *Leskea rigescens* formed a natural group when Bruch and Schimper (1851) described and published the genus *Lescuraea*.

The genus *Pseudoleskea*, also described by Bruch and Schimper (1852), was considered similar to *Lescuraea* particularly in habit and in leaf cell patterns. However, Bruch and Schimper (1852) revealed that these two genera were quite different with respect to the position of the capsule as well as the shape and ornamentation of the peristome. Capsules of *Pseudoleskea* are mostly arcuate, as well as having a hypnobryalean peristome structure. Although Bruch and Schimper did not introduce these terms, they realised there were variations in capsule position and peristome type within natural groups. Consequently, Bruch and Schimper (1852) suggested that *Pseudoleskea*, *Heterocladium* B.S.G., and *Thuidium* B.S.G. belong in the Leskhypnaceae, bridging the gap between the true 'Hypnaceae' and 'Leskeacea'.

Bruch and Schimper (1852) identified two European species, *Pseudoleskea atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G. (= *Lescuraea incurvata* (Hedw.) Loeske) and *Pseudoleskea catenulata* (Brid.) Bruch & Schimp. *in* B.S.G. (initially as

Hypnum catenulata) (= *Pseudoleskeella catenulata* (Brid. *ex* Schrad.) Kindb.), including two North American taxa, *Pseudoleskea congesta* B.S.G. *ex* Par. and *Pseudoleskea liebmanni* Schimp. (= *Rauiella subcatenulata* (Schimp. *ex* Besch.) Wijk & Marg.). Bruch and Schimper (1852) indicated that both *Pseudoleskea atro-virens* and *P. catenulata* had received many names, and had even been mistaken for other mosses, so that synonyms were quite common. Using *Pseudoleskea atro-virens* as an example Bruch and Schimper (1852) stated that this species was found predominantly in exposed areas, and when found in shaded areas had (*sensu* Bruch and Schimper) been erroneously called *Leskea brachyclados* Schwägrichen. As a result, Bruch and Schimper (1852) placed the older name *Leskea brachyclados* in synonomy with *P. atro-virens*. Although Bruch and Schimper had a good grasp on many of the taxa within *Lescuraea* and *Pseudoleskea*, a number of authors (including Bruch and Schimper) had difficulty with several species.

Schimper (1860) described the genus *Ptychodium* for a very large European species with strongly plicate leaves, *P. plicatum* (Schleich. *ex* F. Weber & D. Mohr) Schimper. This species was later transferred to *Hypnum* (Hedw.), *Lesquereuxia* Schimp. *ex* Lindb., and then to the genus *Lescuraea* (Lawton 1957). This species is currently in *Ptychodium* (*fide* Redfearn 1986, Ignatov & Afonina 1992).

Lindberg (1871) revised the spelling of *Lescuraea* to *Lesquereuxia* to better approximate Léo Lesquereux, for which the genus was named. Then Lindberg (1879) listed all species known to occur in Scandinavia under this generic name, namely *Lesquereuxia filamentosa* (Dicks. *ex* With.) Lindb. (= *Lescuraea incurvata*), *Lesquereuxia saxicola* Lindb. (= *Lescuraea saxicola*), and *Lesquereuxia plicata* (Schleich. *ex* F. Weber & D. Mohr) Lindberg (= *Ptychodium plicatum*). Subgenus *Adelphodon*, created by Lindberg in 1872, was to accommodate the single Japanese species *Lesquereuxia robusta* Lindberg. However, Lindberg's (1871) use of the name *Lesquereuxia* was inappropriate since Boissier (1853) had published *Lesquereuxia* previously as a new genus in the Scrophulariaceae (Rohrer 1986). Consequently, Lindberg's (1871) generic name *Lesquereuxia* was invalid. Unfortunately, Fleischer (1923) confused the issue by recognising both *Lescuraea* and *Lesquereuxia*. In addition, Fleischer believed that the species of subgenus *Adelphodon* were phylogenetically unrelated to the rest of the genus *Lescuraea*.

Sullivant (1872) published notes on *Pseudoleskea radicosa* (Mitt.) Macoun & Kindb. (= *Lescuraea radicosa*) and *Pseudoleskea rigescens* Lindb. (= *L. stenophylla*), wherein he stated that the latter specimen is merely a variety of the former. Sullivant (1872) suggested that *P. radicosa* var. *gracilior* (= *L. stenophylla*) connected the type species "a good *Pseudoleskea*," as well as other taxa of *Pseudoleskea*, with those of *Lescuraea*.

Limpricht (1895) followed Bruch and Schimper in retaining the three generic names *Lescuraea*, *Pseudoleskea*, and *Ptychodium*. However, he arranged them in the following way. Within *Lescuraea* were species *L. striata* and *L. saxicola*. *Pseudoleskea* accommodated *P. patens* (Lindb.) Kindb. (= *Lescuraea patens* Lindb.) and *P. atrovirens*. Lastly, *Ptychodium* consisted of: *P. plicatum*, *P. pfundtneri* Limpr. (= *Lescuraea radicosa*), *P. oligocladum* Limpr. (= *Lescuraea radicosa* var. *denudata* (Kindb.) E. Lawton), and *P. decipiens* Limpr. (= *Lescuraea saxicola*). Conversely, Kindberg (1896) retained the genus *Lescuraea* but united taxa in *Pseudoleskea* and *Ptychodium* under *Pseudoleskea* (Lawton 1957).

With many taxa having been reassigned repeatedly between genera, it is important to note that the first revision was not performed until 1900, when Best (1900) took a serious look at the species in North America (Table 2.1). Best (1900) revised seven taxa, and indicated "undesirable as it is in some respects, it becomes necessary to reduce *Lescuraea* to the rank of subgenus." According to Best (1900), "American plants efface the lines of separation between it [*Lescuraea*] and *Pseudoleskea*." To clarify this statement, Best (1900) revealed that the gametophytic characters of *P. radicosa* and *P. rigescens* "connect so closely with those of European Lescuraeas as to leave no doubt of their being congeneric." On the other hand, "the sporophyte characters of *P. radicosa* closely connect with those of *P. atrovirens*, while those of *P. rigescens* do the same with the sporophyte characters of *Lescuraea striata*." Schimper (1876) realised how closely the latter two species were related when he referred to *Pseudoleskea rigescens* under *Lescuraea* as a "species Americanae distinctissima."

Brotherus (1907) separated taxa into *Lescuraea* and *Pseudoleskea*, following Kindberg, and divided *Pseudoleskea* into three sections, *Pseudo-Pterogonium*, *Eu-Pseudoleskea*, and *Orthotheciella* (Table 2.2). Then Arnell and Jensen (1910) united all taxa under *Lescuraea*, with the exception of *Ptychodium plicatum*. Shortly thereafter Mönkemeyer and Brotherus (1925) placed *Ptychodium plicatum* in the Rhytidiaceae, following an earlier system devised by Brotherus. Mönkemeyer (1927) followed the system of Lindberg (1907) and of Arnell and Jensen (1910) by placing all species in *Lescuraea*, with the exception of *Ptychodium plicatum*, using the original spelling of the genus devised by Bruch and Schimper. Based on the structure of the capsules, which were previously unknown, Reimers (1926) assigned section *Orthotheciella* to the Amblystegiaceae. Then in 1929 Thériot demonstrated very clearly that section *Pseudo-Pterogonium* belonged to the genus *Pseudoleskeopsis* Broth. (Lawton 1957).

Of 19 taxa addressed in the second revision of the genus by Lawton (1957), 11 are found both in Europe and in North America (Table 2.1). Lawton (1957) stated that *Pseudoleskea* and *Ptychodium* are heterotypic (taxonomic) synonyms of *Lescuraea*. She accepted the older generic name *Lescuraea*, and recognised three groups of taxa. Consequently, Lawton (1957) devised the following subgenera: *Pseudoleskea*, *Tricholeskea*, and *Lescuraea*. Subgenus *Lescuraea* accommodated *L. striata*, *L. saxicola*, and *L. iliamniana* E. Lawton (= *L. saxicola*), while subgenus *Pseudoleskea* accommodated the rest of the taxa, with one exception. Subgenus *Tricholeskea* accomodated the sole species *Lescuraea baileyi* (Best & Grout *in* Grout) E. Lawton (= *Rigodiadelphus baileyi* (Best & Grout *in* Grout) M. Krieger). According to Lawton (1957), "*Lescuraea baileyi* differs from other species in the genus in having no paraphyllia as well as having hair points on the stem leaves." Lawton (1957) also indicated that "in gametophyte characters *L. baileyi* is not closely related to the other species of the genus, [although], it does resemble *Lesquereuxia robusta* Lindb. (= *Rigodiadelphus robustus* (Lindb.) Noguchi) from Japan in lacking paraphyllia, in leaf shape, in the hair points on the leaves, and in the thick-walled pitted cells." *Lesquereuxia robusta* differed from *Lescuraea baileyi* in having "smooth cells and a radically different peristome" (Lawton 1957).

Lawton (1957) was not first in recognising that *Lesquereuxia robusta* differed from the rest of the species in *Lescuraea*. As indicated earlier, Fleischer (1923) believed this taxon to be phylogenetically unrelated to the rest of the genus *Lescuraea*. Noguchi (1972) proposed the name *Neolescuraea* since *Lesquereuxia* was invalid, and soon realised he had put in synonymy Dixon's (1936) *Rigodiadelphus octoblepharis* and *Neolescuraea robusta*. Given that *Rigodiadelphus* is an earlier name, and Dixon's species is synonymous with Lindberg's *Lesquereuxia robusta*, a new combination *Rigodiadelphus robustus* (Lindb.) Noguchi was made (Noguchi 1972).

Lawton (1957) indicated that the dioicous nature of *Lescuraea*, *Leskeella*, and *Pseudoleskeella* separate them from the other genera in the subfamily. Similarly, *Lescuraea* can be distinguished from both *Leskeella* and *Pseudoleskeella* based on the following characters:

> *Lescuraea* consist of small to large plants, with paraphyllia numerous except in *L. baileyi* and *L. iliamniana*, alar cells predominantly quadrate except in *L. incurvata* where both quadrate and transversely elongate cells are common, peristome teeth united at the base to form a conspicuous dark brown band in subgenera *Pseudoleskea* and *Tricholeskea*, and an inconspicuous yellow to brown band in subgenus *Lescuraea* (Lawton 1957).

Plants in *Pseudoleskeella* are very small to small- or sometimes medium-sized, paraphyllia are lacking, the alar region forms a conspicuous group of transversely elongate cells, and the exostome is without a dark basal band (Lawton 1957). Other distinguishing characters common to both *Leskeella* and *Pseudoleskeella* are: laminal cells with papillae lacking, margins plain and entire throughout, abaxial costa not at all prorate along the upper portion, presence of an annulus, and yellow, nearly linear exostome teeth. Lawton (1957) indicated that the structure of the alar cells in *Leskeella* and *Pseudoleskeella* distinguish them from taxa in *Lescuraea*, except maybe *L. incurvata*. However, other characters such as the absence of an annulus, clearly positions this later taxon in *Lescuraea*.

Whereas Lawton (1957) described 15 taxa of *Lescuraea* in North America, Wijk *et al*. (1964, 1967) enumerated seven valid species in North America less than ten years later. Many of the species revised by Lawton were considered by Wijk *et al*. (1967) to belong to the genus *Pseudoleskea*. The most recent Index of Mosses (Crosby *et al*. 1999), a compilation of Index Muscorum and older versions of Index of Mosses, also lists species in both genera, while others are synonyms of other taxa.

Although there are many specimens that fall in well-defined species, there are an equal number that are highly variable and not so easily defined. Furthermore, peristome differences are partly responsible for the uncertainty in the treatment of taxa in *Lescuraea* and *Pseudoleskea*. Consequently, differences in capsule shape and peristome structure have repeatedly resulted in the separation of taxa into the two gametophytically similar genera, or conversely have united all taxa into a single genus of broad scope. Given that the relationships between taxa remain unclear, uncertainty in the treatment of taxa continues. These problems are not unique to the taxa in question, but rather are common within the Leskeaceae (e.g., between *Leskeella* and *Pseudoleskeella*). The literature clearly emphasizes the need for a revision of *Lescuraea* and *Pseudoleskea*.

The following synopsis re-evaluates the delimitation of *Lescuraea* and *Pseudoleskea*, with a revision of the North American taxa.

2.2. Materials and Methods

Specimens

The material used for the synopsis of *Lescuraea* and *Pseudoleskea* has been kindly made available on loan from the following herbaria: ALA, ALTA, B, BM, BP, CAL, CANM, COLO, DUKE, F, FH, G, GJO, H, JE, MAK, MICH, MO, NY, OSC/ORE, PC, S, RO, UBC, UC/JEPS, US, WTU, Z.

Approximately 2500 specimens were examined in this study. It is important to obtain a large quantity of specimens to ensure adequate representation of each species. In addition, to fully understand all of the variation within a species, specimens must be studied from diverse habitats as well as from diverse geographical areas. Similarly, as much type material was requested and studied as possible, to preclude any errors in species concepts.

Nomenclature

The taxonomic revision of *Lescuraea* and *Pseudoleskea* has included an appraisal of 33 specific and infraspecific names. Many early collectors described species that they or others had picked up while on some botanical foray and as such, many names and synonyms exist (Bruch *et al.* 1851). For example, specimens collected in North America were often described as new species or varieties. This problem stems from the fact that neither Europeans nor North Americans really understood the flora of their own regions, let alone that of other regions. This is evident in the number of synonyms that exist, especially for variable species. Even after the first revision was completed in 1900, Best had listed seven specific and four infraspecific names of *Pseudoleskea* for North America, many of which are synonyms. A summary of my current synonymy of seven valid specific and four infraspecific names in *Lescuraea* for North America, as well as insufficiently known taxa is presented (Table 2.3). Although exclusive to Europe, *L. mutabilis* was also studied due to its similarity with *L. saxicola*. This similarity has often resulted in the two names being erroneously used interchangeably. *Nomina nuda, nomina invalida, nomina illegitima*, and orthographic variants are given in Table 2.4. Excluded names are presented in Table 2.5.

Typification of the species is made in the current revision. In the type citation, protologue information is enclosed in quotation marks. Additional important information from the original description often not included in the protologue such as collector or collection number, is listed in square brackets after the quotation marks.

Fieldwork

A large number of collections were made in June and August of 1999 in Banff and Jasper National Parks in the Rocky Mountains of Alberta, Canada. A two-day helicopter trip in August of 2000 in the Wilmore Wilderness Area northwest of Hinton, Alberta resulted in the first time collection of specimens for that area. However, the majority of specimens were collected in August and September of 2000 from the following Provincial and National Parks in Alberta and in British Columbia: Banff and Waterton Lakes National Parks in Alberta; Mount Seymour and Strathcona Provincial Parks, and Mount Revelstoke and Glacier National Parks in British Columbia.

Many different populations of each species were sampled in any given area. The main objectives were to study and understand the plants in their natural environment, to gain an understanding of the diversity of habitats and substrates on which species are found, and to understand how this affects the morphological expression of that species. By collecting specimens from different areas covering a broad range of habitats, the variation within a species can be better documented.

Species of *Lescuraea* were particularly abundant in subalpine to alpine zones of the Rocky Mountains, where they formed extensive mats on exposed rock outcrops, as well as loose mats on soil among species of *Cassiope*, *Carex*, and assorted grasses. Locality, habitat, substrate, and exposure data along with coordinates were recorded for each specimen collected. My collections are deposited in ALTA.

Measurements

Specimens were studied using a ZEISS (West Germany) compound microscope no. 47 0916-9901/03 as well as WILD Typ (Heerbrugg Switzerland) dissecting microscope no. 181300. Whole stems with branches were hydrated in distilled water so that structures could be removed easily. Leaves were pulled back and off the median region of the stem or branch so that the basal and alar cells, including the leaf decurrencies would remain intact. Leaves from the median region of the stem or branch are most highly developed. These leaves are not the oldest (stem base), nor the youngest leaves (stem apex). Very old or very young leaves often do not display all of the structures (e.g., papillae) or poorly represent the characteristics of the species. The leaves from the median region were then mounted in distilled water on a temporary slide. A similar process was used for removing paraphyllia. Due to the small size of paraphyllia, a section of stem was sometimes mounted as well. Hydrated perichaetial leaves and perigonial bracts were removed, layer by layer and arranged in sequential order on slides.

Measurements of structures on the compound microscope were made with an ocular micrometer calibrated at 63X, 100X, and 400X using a one mm stage micrometer. These measurements were then recorded in µm. Measurements of structures under the dissecting microscope, such as seta and capsule length, were made in the dry condition using a small ruler to the nearest millimetre.

Measurements for all characters were recorded as ranges, representing the lowest and highest values. Frequently occurring measurements for some characters (e.g., leaf and laminal cell length and width) were also recorded using ‘mostly’ to indicate the most common range. Infrequent measurements are enclosed in parentheses using ‘rarely’, ‘rarely from’, or ‘rarely to,’ thereby indicating the extreme value.

Illustrations

Line drawings were made on a ZEISS compound microscope using a 'drawing tube' that was fitted between the rotating ocular unit and the body tube. A single scale bar, representing a different measurement at each magnification, is included with a set of drawings. Also included is a caption of the representative structures drawn. Drawings were made at two magnifications (63X and 400X) using a HB 0.3 mm mechanical pencil. The smaller magnification was used to show leaf shape and size variation (including perichaetial leaves) both within and between species. All other structures were drawn at the larger magnification. Laminal cells were drawn to emphasize lumen shape, size, and ornamentation with respect to cell wall thickness.

Characters that remain constant between taxa are not illustrated (e.g., rhizoids and perigonial leaves).

All illustrations were scanned into the computer using a Plustek Optic pro 9636P scanner. These were then reduced in size and incorporated into plates using CorelDRAW 7.0 (Corel Corporation 1997).

Digital Images

Digital images were taken with a Nikon 990 Coolpix digital camera that was mounted (with the aid of an ocular adaptor) onto the dissecting microscope. Images were taken at 60X, 120X, 250X, or 500X Magnification. Images were downloaded to the computer, reduced in size, and subsequently incorporated into plates using CorelDRAW 7.0 (Corel Corporation 1997).

Scanning Electron Micrographs

Micrographs were taken with a JEOL 6301F Field Emission Scanning Electron Microscope (SEM). The dry sporophytes were placed up against a ridge in the carbon sticker, which was affixed to the SEM stub. The specimens were then 'sputter-coated' with pure gold, and inserted into the vacuum chamber in the SEM. Micrographs were downloaded to the computer and subsequently incorporated into plates using CorelDRAW 7.0 (Corel Corporation 1997).

Habitat

Information from the packet label, including habitat data such as forest type, exposure, elevation, and substrate, was recorded for each specimen wherever possible.

Since a number of specimens had been collected at a time when habitat information was poorly noted, some labels have little or no information other than county, collector, and collection number. Specimens I collected have habitat data as well as latitude and longitude coordinates.

Distribution

For each species or infraspecific taxon, a general summary of the distribution is given. This summary is based on the distribution map created for each taxon in North America. General information for Europe and Asia are included where applicable.

Mapping

All North American specimens used in the revision, on loan from the herbaria cited, are mapped. Where the number of specimens for any given species was large, representatives from each US county or Canadian region (if present) were mapped. The US county system has greatly enhanced the ability of collectors to determine the location of their collections. Likewise, this system has also made mapping of these specimens straightforward. Lack of a county (or similar) system in the studied areas in Canada for the most part, has resulted in collections with more vague locality descriptions, and as such, these were more difficult to map accurately.

Floristic Treatments

Wherever possible, regional treatments that include descriptions, keys, and illustrations of taxa have been reviewed. These treatments help reveal how authors in different regions view species concepts, nomenclature, synonymy, and distributions.

2.3. Taxonomic Concepts

Genus

Bartlett (1940) once suggested, "the generic concept is so useful in classifying knowledge" and "has been … logically and extensively applied in various parts of the world." On a practical level, there is a great need for good generic synopses so that closely related species can be grouped together to allow for in-depth evolutionary studies (Stuessy 1990).

Linnaeus (1737) based his generic concepts on those of others before him (e.g., Tournefort 1700, Plumier 1703), and outlined his approach to generic circumscription in

Philosophia Botanica (1751). Linnaeus (1751) suggested establishing species first, and then synthesizing them into genera. Linnaeus' (1751) approach consisted of searching for three characters:

> 1) the *natural character* giving the complete description of all its features and upon which the classification system should be based; 2) the *factitious character* being a selection of features suitable for discrimination among genera in an artificial system of classification or key; and 3) the *character essentialis* which equated to the features allowing for easiest description (Svenson 1945).

From the time of Linnaeus (1751), the concept of genus has remained relatively stable. According to Stuessy (1990), "the basic concept still is that a genus is an assemblage of species that has more significant features in common among its members than with any other species." A corollary to this is that "there is a greater discontinuity between groups of species than between species (called *hiatus taxonomy* by Singer 1986) (Stuessy 1990)." However, Stuessy (1990) suggested that what has changed are the new comparative data available for making comparisons among taxa for purposes of generic circumscription. Of the five types of data Stuessy (1990) indicated that can be used to delimit genera, he remarked that morphological features continue to be very important.

Although genera are certainly less natural than species in terms of representing an actual discontinuity in the living world, they are important for arranging species. As such, once a number of species of a group are known, other species can potentially be recognised as members of the same genus, even though the species themselves may be unknown (Boivin 1950, Stuessy 1990).

The generic concept has been clear for many groups of species. However, in the case of *Lescuraea* and *Pseudoleskea*, the grouping together of species into one, or the splitting of species into two similar genera, has been the source of debate for well over a century.

Species

The problem of how to define a species has similarly been the subject of debate for decades, and has not yet been resolved. From the earliest species concepts of Plato, Aristotle, Cuvier, and Ray, Linnaeus (1751) based his concept on the idea that all species had been created by God and each one possessed an 'essence' (Svenson 1953, Stuessy 1990). Initially, Linnaeus (1751) believed that the elements of order were fixed and discrete, 'natural' kinds. As he became older, Linnaeus (1753) admitted that variations did occur, albeit God-produced. From these ideas and observations, Linnaeus (1753) created the binomial system of classification (Stuessy 1990).

It was through Darwin's travels that the species concept began to change. As a young man, Darwin began to catalogue the 'natural kinds'. However, during his lifetime as he saw more variation within organisms, combined with his theory of evolution, Darwin (1859) began to feel that species had no boundaries at all. Although these species were extremely plastic and mutable, Darwin (1859) believed them to be real entities and not just mental constructs. Darwin stressed the evolutionary integrity of species through descent from a common ancestor, which is the beginning of the various evolutionary species concepts still in use today (Simpson 1961, Wiley 1978, Stuessy 1990). According to Stuessy (1990), "Darwin's effect upon the species concept may be considered the second most influential idea since Plato inadvertently laid out the foundations for the typological concept."

The need for a species concept to facilitate communication and organisation of information about biological diversity is clear. However, the definition of such a concept is much more difficult to agree upon (Mishler and Donoghue 1982, Donoghue 1985, Mishler and Budd 1990, Baum 1998). Stuessy (1990) identified six current species concepts, including Morphological (based on overall similarities in morphology), Biological (interbreeding capability and genetic isolation), Evolutionary (or ecological, ancestral-descendent sequence based on interbreeding capability), and Cladistic or Phylogenetic (based on synapomorphies).

In a recent survey of botanical monographs published between 1983 and 1993, McDade (1995) highlighted two distinct issues that are potentially part of the 'species problem,' defining species as a category, and delimiting species in practice. McDade (1995) highlighted several biological processes that confound the efforts to delimit species:

> recency of divergence and uncertain fate of lineages that have recently split, mismatch between anagenesis (i.e., accumulation of apomorphies) and lineage

> splitting, hybridization, reproduction exclusively or primarily by asexual means, and genetic phenomena such as transposable elements and concerted gene conversion.

The applicability of a given species concept depends largely on the organisms studied. For example, it has long been known or suspected that certain plants within specific genera hybridize more frequently than other plants within the same genus (McDade 1995). Biologists such as Burger (1975) who study plants known to hybridize frequently have shown that the biological species concept, defined primarily by genetic isolation, cannot be applied to their organisms. Similarly, Mishler and Budd (1990) indicated that many biologists (e.g., Eldredge 1985, Ghiselin 1987, Grant 1981, Hull 1987) seem to believe that species do not exist in asexual organisms, at least in an evolutionary sense. Mishler and Budd (1990) revealed that use of different species concepts results in "different measures of species distinctness" thus having "serious consequences for the recognition of predicted patterns." In a discussion of species as 'taxa individuals,' Mishler and Donoghue (1982) indicated that variation in morphology, ecology, and breeding is large and complex, resulting in discontinuities of varying degree in each of these factors. They also revealed that these discontinuities are often not congruent. More recently, Baum (1998) outlined a 'bottom up' approach to individuation, where connections among the parts determine the boundaries of the whole. Baum (1998) argued that individuation, or the existence of individuals through time, can be compared to a wooden ship where the parts (e.g., planks, mast, etc.) are gradually replaced, so that at all times the ship is still intact. Most would agree that it is still the same ship, even though eventually all parts will have been replaced. Baum (1998) suggested that in order to consider the existence of species individuals through time, "biologists must come to terms with there being a plurality of lineages" and that the "current dogma that species originate at the splitting events needs to be reconsidered."

According to Stuessy (1990) and McDade (1995), both the morphological and biological species concepts are still most commonly used in flowering plants. McDade (1995) suggested that many monographers focusing on morphological differentiation point to problems with the practical application of other concepts. Baum (1998) also pointed out where previous uncertainty of species delimitation could reflect limitations of the taxonomist; "fuzziness arises because the world is not fully cooperative with attempts to force order upon it." As such, species occupying a system of classification are species hypotheses (Baum and Shaw 1995), and we can "never prove the existence of species with certainty (Baum 1998)."

In the revision of *Lescuraea* and *Pseudoleskea*, the morphological species concept is followed and species hypotheses are composed.

Variety

Linnaeus (1751) first used 'variety' as a category below the species level, to recognise environmentally induced variation in plants (e.g., climate, soil, heat, wind, etc.). Linnaeus (1753) commonly used the term in his Species Plantarum, and this was the beginning of its common use in plant systematics (Stuessy 1990). The term variety has often been used interchangeably with subspecies, although there are distinctions between the two terms. According to Stuessy (1990), subspecies are considered "variations hereditarily determined as opposed to environmental modifications or plasticities, which are indicative of varieties," although some would argue otherwise. The rank of subspecies is also used to delimit a species with an allopatric distribution, whereas variety is used to refer to species with a parapatric distribution. Consequently, two basic schools of thought have prevailed: the Californian school (use of subspecies as the primary subdivision of species), and the Eastern school (use of varieties) (Stuessy 1990). In addition, where use of the term variety has been more frequent by plant biologists, zoologists must employ the term subspecies.

In McDade's (1995) survey of botanical monographs, "authors [who used infraspecific categories] were clearly attempting to recognize biologically real entities marked by variation due to partial geographic and/or reproductive isolation." Intergradation and degree of morphological differentiation was used to distinguish these infraspecific taxa from those recognized as species. McDade (1995) also pointed out that very few authors actually discussed the biological phenomena responsible for the high levels of variation seen. However, those that did mentioned both primary (i.e., incipient speciation) and secondary contact (i.e., hybridization following speciation) as possible causes.

Soreng (1991) and Karis (1989) pointed to another reason to use infraspecific taxa: to delimit apomictic lineages within otherwise sexual species, and to distinguish ploidy levels within species with multiple ploidy levels, respectively.

In a final note, McDade (1995) suggested that the heterogeneity of the potential processes involved (e.g., incipient speciation, hybridization, asexual reproduction, polyploidy, ecotypic differentiation, etc.) in blurring species boundaries renders the conclusion of infraspecific differentiation less than fully informative.

The rank of variety is applied to a few taxa within *Lescuraea* that exhibit morphological intergradation, as well as a parapatric distribution. I cannot determine with certainty the biological phenomena that may be responsible for the high amount of morphological variability seen within a species. However, differences in substrate and exposure appear to be important factors. Consequently, this variability may or may not be inherited and/or environmentally caused.

2.4. Morphological Characters

The following gametophytic and sporophytic characters were important for the taxonomic revision.

2.4.1. Gametophytic

Plant Size

Although estimation of plant size without actual measurements can be considered highly subjective, three distinct plant sizes in *Lescuraea* can be seen: small, medium, and large, with some variation in between (Fig. 2.1). Plant size as defined here is not the size of the population or specimen, but rather the delicate nature or robustness of individual plants (stems with their respective branches) within the specimen. Small plants are mostly delicate, lax, and soft. Medium plants have a less delicate or lax appearance and are slightly more robust and stiff. Large plants are not at all soft and lax, but rather very robust and stiff. Individual plant measurements can also be subjective, especially if the researcher is unsure of where to begin measuring stem length. Many of the plants in *Lescuraea* form tight mats, thus making it very difficult to tease out the fragile stems without breaking them in the process. In addition, since plants in *Lescuraea* are monopodial the stem continues to grow, thereby making it difficult to ascertain the correct 'length' or to compare stems. However, even stems of mosses that have a sympodial growth form may be difficult to measure accurately. Due to these problems, I decided to use the subjective appearance of size that is based solely on the delicate or robust nature of the plants.

Colour

Species in *Lescuraea* display a range in dominant colour from yellowish to green-brown, with these intermediates: yellow-green, light green, green, dark green, yellow-orange, and orange-green. A characteristic that is typical of species in this genus is the gradual change in colour from those listed above, to an orange-brown or dark brown coloration of the stem as one moves from the distal and younger end toward the proximal or older end of the stem.

The variation in dominant colour between species may be attributed to habitat, specifically exposure to sunlight. In addition to the multitude of herbarium specimens examined, personal collections revealed the following trends. Species inhabiting the branches of shaded shrubs or shaded rocks in upper montane to subalpine forests tend to be yellow-green to light-green, with a more gradual decrease in these dominant colours to a somewhat brown to light brown coloration in older parts of the stem. Species inhabiting cliff faces in somewhat more open subalpine forests, or near significant sources of water (e.g., streams) are green to dark-green. Species growing among heaths in alpine tundra are yellow-green with older stems yellow-brown. Lastly, species inhabiting exposed soil as well as exposed rocks and outcrops in subalpine to alpine areas are yellow-green (with orange tinges) to orange-green, with a more sudden orange-brown to dark brown or black coloration of the stem. It would appear that as plants are increasingly exposed to sunlight, cold temperatures, and the drying effects of wind, they attain more orange coloration in their leaves and stem.

In conjunction with plant colour is the relative lustre or dullness of the leaves, such that plants in *Lescuraea* are lustrous, satin-glossy, somewhat dull, or distinctly dull in appearance. The amount of lustre is a factor of leaf cell size, papillosity, and chlorophyll content. Longer, less chlorophyllose cells with indistinct prorae make the leaf, and thus the plant appear lustrous; while isodiametric, highly chlorophyllose cells with distinct papillae on the cell lumen make the leaf and plant appear dull. The light that is refracted from short papillose cells is scattered, as opposed to the unscattered refracted light from smooth cells, thus making the leaf appear dull. The relative lustre of plants is best seen under the dissecting microscope.

Life and Growth Form

The terms life form and growth form have often been confused. As a result, both have been used interchangeably in the past to signify the same thing. Meusel (1935), Mägdefrau (1982) and LaFarge-England (1996) reviewed the terminology of these two terms in detail. Where life form refers to the overall growth pattern of the population, growth form refers to the pattern of growth of the individual plants that form the population (Mägdefrau 1982). However, these concepts are not as simple as they seem. LaFarge-England (1996) thoroughly reviewed these concepts in mosses and described in detail the many branching patterns in mosses.

The life forms of taxa in *Lescuraea* are quite similar, and include dense to loosely intertwining mats and wefts. Mats are defined as densely interwoven, horizontal life forms, while wefts are characterised as loosely interwoven, often ascending life forms (Magill 1990). The somewhat loose to distinctly dense intertwining mats found on bark as well as on shaded and exposed rocks respectively, have abundant rhizoids. In contrast, wefts are found growing on soil among *Cassiope* sp., *Carex* sp., and Poaceae, as well as on soil over boulders often among other bryophytes, and have very few to no rhizoids.

The growth forms in *Lescuraea* include prostrate stems with few or no branches to highly branched individuals. These branches are often suberect to erect. Since there is little difference in appearance between main and lateral shoots, that is stems and branches (with their respective leaves) are similar in shape though not always in size, species with this growth form have often been referred to as 'Thread mosses'. This growth form is found in most of the Leskeaceae (Mägdefrau 1982).

Stems (main shoots)

As indicated earlier, stem length was not measured but rather plant size was estimated based on the lax or robust appearance of the plants. Stems of lax species are slightly round in transverse section, whereas robust species clearly display an elliptic (or flattened) appearance. That is not to say that stems of lax species are never elliptic, since this condition is also present. Stem transverse sections of smaller, lax plants generally become round upon wetting, while stem sections of larger, more robust species tend to keep their elliptic condition even upon wetting.

The structure of the stem may influence whether stems are slightly round or distinctly elliptic. Stems of smaller, lax species tend to have fewer thickened outer cortical cells (1-2 layers, rarely 3 in some places), with a somewhat abrupt change to large or very large-lumened, thin-walled hyaline cells of the medulla. Stems of larger, more robust species tend to have more numerous thickened outer cortical cells (3-4 layers, rarely 2 in some places), with a more gradual increase in size of the large-lumened hyaline cells of the medulla (Fig. 2.2). It is possible that in species with fewer outer cortical cells, inner hyaline cells are able to expand upon wetting, and thus take on a more round shape. In species with more numerous outer cortical cells, the thicker-walled inner hyaline cells may be less able to expand, thus affecting the shape of the more rigid outer cortical cells. Despite differences in size and number of outer and inner cortical cells, all species have a differentiated central strand of smaller-lumened, somewhat angular cells. Occasionally, *Lescuraea patens* has a poorly differentiated central strand, although it is present.

Branches (lateral shoots)

The type of branching discussed under growth form is what LaFarge-England (1996) referred to as 'monopodial'. In monopodial branching, "branches are produced along the main axis by subsidiary, lateral innovations; forming a series of unconnected 2° to 3° modules along a 1° or 2° module, respectively (LaFarge-England 1996)." According to this terminology, most species of *Lescuraea* have few irregularly positioned 2° modules (branches) along a 1° module (main stem). However, several taxa (*L. patens*, *L. atricha*, *L. mutabilis*, and *L. saxicola*) often display numerous irregularly positioned 2° and 3° modules along a 1° or 2° module. These 2° or 3° modules (branches) are relatively short in *L. patens* and *L. atricha*, and quite long in the latter two species.

Rhizoids

Tuomikoski (1958) first introduced the term 'rhizoid topography', which refers to the pattern of rhizoid locations on the stems and leaves of mosses. According to Koponen (1982), there are at least five basic types of rhizoid topography, which are based on studies carried out on two families, the Mniaceae and Amblystegiaceae. In the first type, rhizoids originate on leaves, while in the second and third types; rhizoids originate along the stem without having any special location or originate at the leaf axils from the cells surrounding the branch primordia, respectively. In the fourth type, rhizoids concentrate in dense bunches on the ventral side of the stem just at or below the insertion of the costa. Lastly, in the fifth type rhizoids are absent.

Rhizoids are similar in structure and in colour between species in *Lescuraea*, and correspond with Koponen's (1982) fourth rhizoid type. All rhizoids are smooth, red-brown to deep red, and relatively unbranched. In taxa where rhizoids develop along the entire or a large portion of the ventral side of the stem including the lower costa, they are red-brown in colour and highly branched, causing a matted and continuous tufted appearance. However, in species where rhizoids are limited to the ventral side and distal portion of the stem, they form a small, relatively unbranched, and lustrous pendulous tuft, which has a deep red to red-brown coloration. In addition, several taxa produce few or nearly no rhizoids (e.g., *L. incurvata* var. *gigantea* and *L. radicosa* var. *denudata*), although when present, appear similar to rhizoids of other taxa in *Lescuraea*.

Koponen (1982) suggested that rhizoid topography is a rather stable character, "so that all the species of a certain genus have a similar rhizoid topography."

Paraphyllia

Hedwig (1801) was among the first to describe and illustrate paraphyllia. He referred to them as 'stupae' (Latin, meaning tow hemp or coarse flax), since they looked fibrose at low magnifications. Hedwig (1801) did not understand the function of what he had seen, since he described them as secondary radicles and placed them in the glossary under the general heading 'Radix.' Wilson (1855) defined 'villi' (Latin, meaning long weak hairs) as "jagged or branched leafy processes covering the stem amongst the leaves, distinguished from radicles by their shape and by their green colour." Boulay (1872) simply referred to them as accessory leaves. The term 'paraphyllia' (Greek, *para*, beside; *phyllon*, leaf) was used by Bruch *et al.* (1836-1855), although it may not have originated at this time. The term 'paraphyllia' is used today.

Paraphyllia, unistratose chlorophyllose ecostate organs that vary greatly in size and form, are found covering stems and branches of many pleurocarpous families

(Ireland 1971). Paraphyllia can be branched or unbranched and filamentous, to unbranched and distinctly foliose, with many forms in between. Pseudoparaphyllia as the name implies, are 'false' paraphyllia. Pseudoparaphyllia are not found covering stems and branches, but rather are restricted to branch primordia and bases of mature branches. Where "filamentous paraphyllia can be branched and cells smooth or papillose, neither the filamentous-branched type nor the papillose cells occur among the different types of pseudoparaphyllia (Ireland 1971)."

All species in *Lescuraea* have some type of paraphyllia (Fig. 2.3). Filamentous and foliose paraphyllia tend to be numerous on both stems and branches, and often even more plentiful on younger portions of either. Filamentous paraphyllia, which range from several to numerous cells in length, can often be seen on transverse sections of stems. When they become quite long, they are evident under the dissecting microscope as well. The forms of foliose paraphyllia are quite variable both within and between species, such that it is difficult to predict patterns. Foliose paraphyllia may be narrowly lanceolate to broadly lanceolate, distinctly incised or cleft, or not at all incised or cleft. The incisions, which are often near the bases of paraphyllia, make paraphyllia appear as though they are branching (when in fact they are not). Although branched paraphyllia are numerous on taxa of *Thuidium* and *Heterocladium*, they are rare in *Lescuraea*. *Lescuraea mutabilis* and *L. radicosa* var. *denudata* are the only taxa in *Lescuraea* to have narrowly lanceolate or filamentous and truly branched paraphyllia. *Lescuraea atricha*, *L. radicosa* var. *radicosa*, and *L. radicosa* var. *compacta* have small filamentous, slightly branched paraphyllia as well as unbranched foliose paraphyllia. Cell lumen shape within foliose paraphyllia also appears to vary somewhat between taxa. Cells may be elongate, rectangular, rhomboidal, isodiametric, and ± thick- or thin-walled. These cells may also be somewhat prorate in *L. atricha* and in the *L. radicosa* complex, causing the paraphyllia to appear somewhat dentate.

Paraphyllia clearly originate from cells on the outer cortex that are identical between taxa in *Lescuraea*. These cells can be clearly seen on transverse sections of stems, giving rise to small paraphyllia. *Pseudoleskea arizonae* Williams (= *Pseudoleskeella arizonae* (Williams) E. Lawton), was transferred to *Pseudoleskeella* by Lawton (1957) due to a lack of paraphyllia as well as other distinguishing characters.

Wilson and Norris (1989) revised the taxa of *Leskeella and Pseudoleskeella* and placed this taxon back into *Lescuraea*, claiming to have seen the cells that give rise to paraphyllia. It is possible Wilson and Norris mistook leaf decurrencies for filamentous paraphyllia in this taxon, since neither paraphyllia nor the cells that give rise to paraphyllia were seen on any specimen that I examined. Leaf decurrencies that remain attached to the outer cortex after leaves are removed for viewing are often confused for paraphyllia, and this needs to be taken into account. Therefore, it is evident that this taxon belongs in *Pseudoleskeella* and not in *Lescuraea*. On the other hand, the status of *Lescuraea saxicola* remains unclear. Specimens examined from Europe, eastern North America, and several western provinces and states including southern British Columbia and Alberta, display numerous large filamentous as well as foliose paraphyllia along stems and branches. However, specimens examined from northern British Columbia, Alaska, and Asia, appear naked in contrast. Specifically, only very few paraphyllia were observed on Alaskan and several Japanese specimens. However, numerous filamentous and foliose paraphyllia were observed in and around stem and branch leaf axils. In contrast, specimens identified as *Lescuraea julacea* Besch. & Card. *in* Card. (= *L. saxicola*, *fide* Noguchi 1972, Noguchi *et al.* 1991) from Japan did not have any paraphyllia, although cells that give rise to paraphyllia are seen on transverse sections. These cells possibly represent vestigial remnants of once much larger paraphyllia. In addition, numerous deltoid and narrowly lanceolate pseudoparaphyllia are observed around branch primordia on stems as well as on branches. Interestingly, these same pseudoparaphyllia are seen on specimens of *Lescuraea iliamniana* from Alaska. Lawton (1957) concluded that, "paraphyllia [were] absent in this species, or that a few were restricted to where branches originate." What Lawton had described were actually pseudoparaphyllia and not paraphyllia. Pseudoparaphyllia, common in species of *Pseudoleskeella*, have not been previously identified or described in taxa of *Lescuraea*. Upon closer examination of *Lescuraea saxicola* from Europe, it is noted that several specimens are also devoid of paraphyllia. However, cells that give rise to paraphyllia are clearly visible on stem transverse sections. Where *Lescuraea julacea* is described from Japanese specimens with few to no paraphyllia, the frequency of paraphyllia of *L. saxicola* (from numerous to lacking) varies greatly not only in Japan but also in North

America and in Europe. Since no other differentiation between the two species is observed and their distribution is sympatric, *L. julacea* is once again placed in synonymy with *L. saxicola*.

Stem Leaves

The habit, shape, colour, and arrangement of stem (main shoot) and branch (lateral shoot) leaves are what give species in *Lescuraea* their characteristic appearance. The dry leaf habit ranges from erect-appressed to julaceous, and is straight, slightly falcate or distinctly falcate secund. Leaf shape ranges from linear-lanceolate, lanceolate, ovate-lanceolate, ovate, and ovate-acuminate (Fig. 2.4). The distal end of the leaf forms an acumen that varies somewhat in shape within and highly between species, but varies also with respect to the length of the leaf proper. The shape of the acumen ranges from gradually short or long acuminate, abruptly short or long acuminate, to somewhat acute. The acumen may be distinctly longer, equal to, somewhat shorter, or distinctly shorter than the length of the leaf proper.

Leaf length ranges from 0.6 mm (*Lescuraea patens*) to 2.4 mm (*L. radicosa* var. *denudata*) long and from 0.2 mm (*L. saxicola*) to 1.0 mm (*L. radicosa* var. *denudata*) wide. Leaf length is measured from the apex to the base of the leaf, where the costa and the basal cells attach to the stem. Leaf decurrencies, which extend down from the alar region, are not included in measurements of leaf length. Leaf width, which is measured at the widest point (approximately mid-leaf or somewhat lower) of the leaf, includes the recurved margins. Inclusion of the extent of the recurved leaf margin is important since it varies between species. Not including this measurement would suggest that some species have narrow leaves when in fact they do not. A number of leaves are measured from several stems and branches within a given specimen, to represent the range of leaf sizes in the median region. This is repeated with a large number of specimens, to determine the range and most common measurements.

Leaf Margins

Leaf margins are entire, from the leaf base to the lower acumen. The middle to upper acumen is indistinctly or distinctly serrate, slightly dentate, or rarely entire. The margins of the acumen are predominantly serrate or dentate due to projecting cell wall ends (prorae), although the shape of the marginal cells is also a factor.

The degree of recurvedness between species is such that leaf margins may be variously recurved from the upper or lower acumen to the leaf base, with gaps of plane margin frequently present throughout. The leaf margins may be more or less recurved on one or both sides, and sometimes one side is not at all recurved. The margins, whether recurved or not, are included in the measurement of leaf width.

Costa

In taxa of *Lescuraea*, the costa varies in length, width, and shape. Costal length in most taxa ranges from subpercurrent to distinctly percurrent. In a few taxa, the costa ends in the lower to mid acumen. Costal width ranges from narrow to very stout in the lower leaf region, becoming narrow and dissipating in the middle or upper acumen, or remaining stout, and ending abruptly as an acute point in the lower acumen. The shape of the costa, which refers to its appearance on the dorsal surface of the leaf, varies from indistinctly keeled in some taxa, to distinctly keeled in others. The keeled costa, which is similar to the keel of a boat, together with leaf shape, gives the leaf an appressed or julaceous appearance.

The upper abaxial portion or tip of the costa may also be variously prorate. In taxa with a long slender costa, the upper abaxial portion is only slightly to somewhat prorate. In taxa with a long and yet more robust costa, the upper portion is usually strongly prorate. Generally, taxa with a shorter and more robust costa have a greatly prorate upper abaxial region.

The costal anatomy of taxa in *Lescuraea* consists exclusively of large, highly vacuolated, thin-walled and longitudinally arranged guide cells that are part of conducting parenchyma. Stereids, which are small, slender, and elongate, thick-walled fiber-like cells found in groups (stereid bands), do not occur in *Lescuraea*. The costal anatomy does not vary within or between taxa in *Lescuraea*, and as such is not included.

Laminal Cells

There are four laminal cell types: alar, basal, median, and distal. The alar region consists of non-papillose, predominantly thick- or thin-walled cells that vary from quadrate, transversely elongate, oblong-elongate, somewhat enlarged quadrate or enlarged oblong (Fig. 2.5). The alar region is very small in some species (several cells wide along the base and restricted to a few cells up along the margin) and large in others (numerous cells wide along the base and extending far up along the margin). The extent of the alar region is reflected by the size of the leaf, such that a small region occupies a small area of the leaf whereas a large region occupies a larger portion of the leaf. The decurrencies at the base of the alar region may be short and somewhat narrow, to long and narrow.

The basal region is somewhat more difficult to define since these cells lead into the transition and median cells. The lowermost 4-6 rows are quite homogenous and are considered the basal region in this study. The basal cells range from quadrate, oblong, enlarged quadrate or rectangular, to linear-fusiform, and are variously thick- or thin-walled, somewhat to distinctly pitted, or not at all pitted (Fig. 2.6). Alar and basal cells described as enlarged are thin-walled, resulting in cell lumina that appear lax and quite broad. These lax cells are not to be confused with the term 'inflated'.

The median and distal region consists of the most variable cells within taxa of *Lescuraea*. Generally, median cells vary somewhat in shape from the costa to the leaf margin. Included in measurements are cells adjacent to the costa and cells extending into the middle to upper median region of the leaf proper. Cells within several rows of the margin were not measured since they are often extensions of the alar region. The median region consists of cells with the following shapes: isodiametric; oval; short- and long-rhomboidal; oblong-rectangular; fusiform; fusiform-linear; and linear, and are variously thick- or thin-walled, pitted, or not at all pitted (Fig. 2.7). The distal region extends from the lower acumen (the area where the leaf proper first begins to narrow more rapidly) to the leaf apex. Distal cells are similar in shape to median cells, varying to some extent within, but mostly between species. Measurements of distal cells include cells of the lower acumen, and well into the upper acumen and apex.

To reveal differences in cell wall thickness and lumen shape, measurements of cell lumen length and width were favoured in place of cell wall measurements. Measurements of cell length are taken from the upper to lower end of the cell lumen and do not include the cell walls. Cell width measurements are taken from the mid-region (or the widest point, excluding pits) of the cell lumen. The inclusion of cell walls in measurement of cell length and width, in many cases, would have lead to similar-sized cells between species, and not have taken into account lumen size.

Papillae

Papillae, which are common in most species of *Lescuraea*, are solid microscopic protuberances on cell lumina or over cell ends. The type, location, and frequency of papillae vary between taxa in *Lescuraea*. However, only a single papilla is ever present on any given cell surface. They may be present as a small and rounded or moderately long single papilla on the centre of the cell lumen, as a rounded papilla on the upper cell lumen, or as a rounded extension (prora) of the upper cell wall (Fig. 2.8).

Papillae occur on both stem and branch leaves, although more commonly on the latter where they are evident on some median and most distal cells. A few taxa also have lower median and alar cells that are papillose or prorate. In contrast, basal cells are never papillose or prorate. The frequency of papillae and prorae varies greatly between species, yet is rather stable within species. While leaves of some taxa have very few to no papillae or prorae, others have many.

Lawton (1957) stated that some species only have papillae or prorae on the abaxial leaf surface, while others have them on both the abaxial and adaxial leaf surfaces. Upon examination of taxa in *Lescuraea*, this finding was not substantiated. It would appear that papillae and prorae are found on both abaxial and adaxial surfaces of stem and branch leaves.

Perichaetia

All taxa in *Lescuraea* are dioicous, with perichaetia common or rare on female plants. Nevertheless, perichaetial leaves are of two types (Fig. 2.9). The first perichaetial leaf type found in all but one species, appears satin-dull and translucent. In this type, the outer and inner perichaetial leaves are somewhat to distinctly erect throughout. The second perichaetial leaf type, found only in *L. saxicola* and *Rigodiadelphus* spp., appears quite lustrous and opaque. In this second type, both outer and inner perichaetial leaves are somewhat to distinctly squarrose above mid-leaf.

Perichaetial leaves in most taxa of *Lescuraea* are quite similar in shape and size, although there are differences that correspond to the two types (Fig. 2.10). In the first and most common type mentioned above, the inner perichaetial leaves are mostly linear-lanceolate, somewhat plicate, and somewhat or abruptly contracted to a short or long acumen. The acumen is often long and narrow, and somewhat serrate. Inner perichaetial leaves clasp the seta below and the acumina adhere to or are parallel to the seta. The costa of the inner perichaetial leaf is distinct, ending well into the acumen, or distinctly excurrent.

Perichaetial leaves in *Lescuraea saxicola* and *Rigodiadelphus* spp., are lustrous, broadly lanceolate, smooth, and abruptly contracted to a short or rarely somewhat long acumen. The margins of the acumen are not at all or sometimes only slightly serrate. In this type, leaves are loosely cucullate or concave, clasping the seta below, and spreading or even squarrose above. The costa of the inner perichaetial leaf is very weak and narrow, ending mid-leaf or well below.

The laminal cells of perichaetial leaves are different from cells of stem or branch leaves in that they all form long rectangular, lax to slightly inflated, hyaline basal to lower median cells. These cells form an oblique region that extends from the costa up toward the margin. Median and distal cells are chlorophyllose or echlorophyllose and are rhomboidal-fusiform, flexuose, to linear. Laminal cells of the first perichaetial leaf type mentioned above are mostly rhomboidal to somewhat fusiform, whereas cells of the second leaf type are always linear.

Hedenäs (1989, 1999*a*, *b*) found identical perichaetial leaf types among other pleurocarpous taxa; revealing statistically that phylogenetic history and not environment, is largely responsible for explaining these character states (Hedenäs 1999*a*, *b*).

Perigonia

Perigonia, which are bud-like and orange-brown for all taxa in *Lescuraea*, are either occasional or common on male plants. In only one species (*L. stenophylla*) are perigonia common, often with ten or more perigonia present on a single stem. In the remaining taxa, perigonia are occasional, with fewer than three quite typical. Only *L. mutabilis* compares somewhat with that of *L. stenophylla*, commonly with more than five perigonia on male plants.

Perigonial bracts are quite similar for all species, ovate and short acuminate and with the upper acumen slightly serrate. The oblong to rectangular basal cells, which are slightly lax and orange-hyaline, also form an oblique region in the lower portion of the leaf, extending to the margin. Median and upper cells are rhomboidal-fusiform or linear.

Inner perigonial bracts are thin and narrowly costate or ecostate. Outermost perigonial bracts are mostly ecostate for all species. Paraphyses are present between the antheridia.

2.4.2. Sporophytic

Sporophytes are common, occasional, or rare in taxa of *Lescuraea*. Although gametophytic, the calyptra is included here due to its involvement in the development of sporophytes. The presence of calyptras on capsules is extremely rare in *Lescuraea*. However, they are cucullate and smooth for all taxa.

Seta

The setae are smooth for all taxa in *Lescuraea* and vary in colour from yellow, yellow-orange, orange-brown, orange-red, and red-brown. When viewed from the top they are somewhat to conspicuously dextrorsely twisted below and sinistrorsely twisted above. The seta is quite thin in *Lescuraea mutabilis*, *L. saxicola*, and *L. stenophylla*, while in the other species it is somewhat more robust. Seta length varies from 0.5 cm to 1.5 cm.

Capsule

Capsule shape and orientation in *Lescuraea* range from: arcuate, cylindric and asymmetric; suberect, cylindric and asymmetric or symmetric; and erect, cylindric and symmetric (Fig. 2.11). The variation in colour is from deep red-purple, red-brown, orange-red, orange-brown, orange, to orange-yellow. Most mature capsules are slightly rough and dull in appearance and are conspicuously constricted below the mouth when dry. This constriction causes the mouth of the capsule to flare outward, revealing the peristome. Mature capsules of *L. mutabilis* and *L. saxicola* on the other hand, are more commonly smooth and lustrous, and not at all constricted below the mouth when dry. As a result, the mouth does not flare outward and the lower portion of the peristome is concealed. Capsules in *Lescuraea* range in size from 0.05 to rarely 0.2 cm long, and are considerably shorter than capsules of *Leskea*, which are typically between 0.2 and 0.3 cm long. Stomata, which are present in all taxa of *Lescuraea*, are found at the bases of capsules. Hedenäs (1989, 1999*a*) has found stomatal pore shape variation within the pleurocarpous taxa, ranging from round to distinctly long pored. All taxa in *Lescuraea* appear to have round-pored stomata.

Operculum

All taxa in *Lescuraea* are stegocarpous, where opercula are conic, short, or obliquely short rostrate, or somewhat long rostrate. However, all taxa lack an annulus joining the operculum to the capsule mouth. The lack of an annulus clearly distinguishes taxa in *Lescuraea* from most other taxa in the Leskeaceae.

Peristome

The peristome in taxa of *Lescuraea* is inserted along the mouth of the capsule and somewhat 'hypnobryalean', or deeply inserted below the mouth of the capsule and variously reduced.

Hypnobryalean peristome:

Most taxa in subgenus *Pseudoleskea* are said to have a 'hypnobryalean' peristome. This peristome consists of a well-developed exostome and endostome, resembling that of taxa in the genus *Hypnum*. The outer peristomial layer (OPL) of the typical 'hypnobryalean' exostome tooth contracts abruptly at the point of contact with the endostome, making the tooth appear 'shouldered'. The 2° cell wall thickenings (as fine horizontal striae that extend to ⅔ the height of the tooth) as well as the cells of the OPL give the lower part of the tooth this broad shouldered appearance. A median divursal line extends up through these 2° thickenings in a 'zigzag' fashion. The distal end of the hypnobryalean exostome tooth has large and rounded, sparsely distributed papillae, as well as a sharp apex. The primary peristomial layer (PPL) forms wide and distinct trabeculae along the entire ventral surface of the tooth. Although wide, these trabeculae do not extend to the edges of the OPL. As a result, the exostome tooth appears bordered. Generally, hypnobryalean exostome teeth are inserted along the mouth of the capsule and are rather greatly inflexed or incurved (Fig. 2.12).

Hypnobryalean endostome segments, which are as long or longer than the exostome teeth, are distinctly keeled, highly perforate along the median line, and have a high basal membrane with cilia. The PPL, which also forms the dorsal surface of the endostome, is variously papillose, and beset with fine and narrowly spaced horizontal lines that are visible under the compound microscope. These lines correspond to the trabeculae of the exostome. The inner peristomial layer (IPL), which forms the ventral surface of the endostome, consists of broad sections where the joints are distinctly thickened.

When the dorsal surface of the endostome is viewed through the compound microscope, both fine lines and thickened joints are easily seen through the yellowish-translucent segments. It has long been thought that the endostome is unilayered and formed solely from the IPL (Robertson 1941, Kreulen 1972, and Mueller 1973). However, Philibert clearly exhibited (at the end of the nineteenth century) the endostome to be a two-layered structure (Taylor 1962). More recently, Shaw and Rohrer (1984) revealed through a scanning electron microscopy (SEM) study of endostomial architecture, how part of the PPL and IPL form the endostome.

Most taxa in subgenus *Pseudoleskea* have only slightly shouldered exostome teeth, with the majority more gradually lanceolate throughout (Fig. 2.13). The 2° cell wall thickenings of the OPL do not form fine horizontal striae, but rather create an undulating surface here referred to as papillose-striae. The 2° cell wall thickenings extend to nearly ⅔ the height of the tooth in *Lescuraea patens* (subg. *Pseudoleskea*). In all other taxa, these thickenings only extend from ¼ to rarely ½ the height of the tooth. The distal portion of the tooth has large and rounded, sparsely distributed papillae. In addition, the apex is usually blunt. The endostome segments are keeled or terete, and arise from a high, medium, or low basal membrane (Fig. 2.14). Cilia are somewhat long and filiform in a few taxa, but mostly short and broad, rudimentary, or lacking altogether. This peristome is in contrast to the distinctly hypnobryalean peristome of *Hypnum*, and to a lesser extent of the Thuidiaceae (wherein *Pseudoleskea* has sometimes been placed).

***Isobryalean peristome*:**

In contrast to the 'hypnobryalean' peristome, taxa in subgenus *Lescuraea* are traditionally said to have an 'isobryalean' peristome to explain their somewhat or much reduced exostome and endostome. Characteristics of the typical isobryalean peristome include the following. The exostome teeth are normally pale, linear, and not shouldered below; the OPL is often highly papillose or smooth throughout, or sometimes with horizontal striae below; and the trabeculae are often low and as wide as the OPL, dramatically minimizing the border between the OPL and PPL. The endostome segments are narrow while the basal membrane is normally low. Lastly, cilia are lacking and spores are often large.

Taxa in subgenus *Lescuraea* have exostome teeth that are erect and inserted well below the mouth of the capsule, and the basal membrane is often found adhering to the exostome. The exostome teeth are mostly linear, and the 2° thickenings form horizontal ridges (as opposed to fine striae or papillose striae) that reach from ¼ to nearly ⅓ the height of the tooth (Fig. 2.13). The distal portion of the tooth has small, coarse, and densely distributed papillae, and the apex is blunt. This ornamentation is in contrast to the papillose or nearly smooth OPL surface typically associated with isobryalean peristomes of taxa in the Leucodontales, for example. Trabeculae in *Lescuraea* are often low and as wide as the OPL surface. As a result, the tooth does not appear bordered. The endostome segments, which are filiform and densely papillose throughout, are joined to form a low or very low basal membrane lacking cilia (Fig. 2.14).

***Reduced hypnobryalean peristome*:**

Lescuraea stenophylla (subg. *Pseudoleskea*) has never been considered to have a true 'hypnobryalean' or 'isobryalean' peristome. Rather, this epiphytic taxon features peristomial characteristics commonly associated with both peristome types.

It is believed that this taxon and other species normally included in subgenus *Lescuraea*, feature reduced peristomes that are not 'isobryalean,' as adaptations to increasingly epiphytic and more xerophytic habitats. Reduction has occurred repeatedly within moss evolution and has been well documented in a number of unrelated families by, for example, Vitt (1981), Buck and Vitt (1986), and more recently by Buck *et al.* (2000).

Characteristics of a reduced peristome are as follows. The OPL is often indistinctly 'shouldered'; the OPL 2° cell wall thickenings remain quite low; a greater proportion of the tooth is highly papillose; the tooth apex is rounded or truncate; the median divursal line is less evident but still 'zigzag' in most (Fig. 2.13), and the PPL often forms indistinct and low trabeculae. The endostome segments are variously shorter than the exostome, are terete, filiform, or lacking altogether, and are indistinctly perforate; the basal membrane is low; and cilia are absent or vestigial remnants are visible (Fig. 2.14).

As indicated earlier, reduction is associated with a change in habitat and substrate, from primarily terricolous to corticolous or even saxicolous. In a reduction series the endostome is often reduced before the exostome, with cilia being lost first, then segment reduction and lowering of the basal membrane, finally with segment loss (Vitt 1981, Buck and Vitt 1986, Buck *et al.* 2000).

Reduction as defined above, is already evident in several epiphytic taxa in subgenus *Pseudoleskea*, of which *Lescuraea stenophylla* and *L. saviana* are examples. In these taxa, endostome segments are narrowly keeled or terete, the basal membrane is low, and cilia are lacking or rudimentary. A lowering of the basal membrane and loss of cilia are also evident in saxicolous taxa, such as *Lescuraea radicosa* var. *radicosa* and *L. incurvata* var. *incurvata.*

Ornamentation:

The ornamentation of the exostome, produced by the OPL, PPL, and 2° cell wall thickenings, is a valuable character at both the infrageneric and specific levels. The proportion of the 2° cell wall thickenings (producing the striae and ridges) of the OPL that extend up the height of the exostome varies somewhat or greatly between species (Fig. 2.15). These thickenings are horizontally finely papillose-striate (rarely horizontally finely striate) in the proximal region of most taxa in subgenus *Pseudoleskea*, or horizontally broadly ridged in subgenus *Lescuraea*. However, *L. saviana* and occasionally *L. stenophylla* (both subg. *Pseudoleskea*) also feature somewhat broadly ridged striae in the proximal region. The mid-tooth region of the exostome is papillose-striate in an oblique or circular fashion, to finely papillose in subgenus *Pseudoleskea*, or papillose-striate to coarsely papillose in subgenus *Lescuraea.* The upper tooth has large, rounded, and sparsely distributed papillae in subgenus *Peudoleskea* and small, coarse, and densely distributed papillae in subgenus *Lescuraea*.

The ornamentation and shape of the endostome produced by the PPL and IPL, including development of the basal membrane and cilia, are also important characters. Endostome segments (as noted above) are distinctly keeled, narrowly keeled or terete, or filiform. The size and concentration of papillae on the PPL range from minute and somewhat sparsely papillose in most taxa in subgenus *Pseudoleskea*, to somewhat large and densely papillose in subgenus *Lescuraea*. Frequently, papillae are also larger and more densely distributed on segments in *L. stenophylla*. SEM images of endostome segments reveal small and slightly forked or small rounded papillae on the PPL, and elaborate forking papillae on the IPL of taxa in subgenus *Pseudoleskea*. Papillae on both the PPL and IPL of taxa in subgenus *Lescuraea* appear to have forks compressed in a short and thus coarse-appearing stature.

Spores

Spore size and architecture ranges from 9.6 µm and minutely papillose to 24 µm and coarsely papillose, with *Lescuraea mutabilis* and *L. saxicola* having consistently large and coarsely papillose spores.

2.4.3. Ecology

All taxa of *Lescuraea* are mountain inhabitants in western North America, with several disjunct taxa in areas of higher relief in eastern North America. Most taxa have a Holarctic distribution. However, only two taxa are endemic to western North America. The elevational range in taxa of *Lescuraea* is from 300-3350 metres, with the majority inhabiting elevations in excess of 1200 metres. Exposure ranges from full shade in montane forests, partial shade of subalpine forests and heath tundra, to full exposure on rocks and outcrops in subalpine clearings and alpine tundra.

Taxa of *Lescuraea* are predominantly saxicolous, growing on shaded and exposed siliceous (less commonly so on calcareous) rocks and rock outcrops in montane to alpine areas. *Lescuraea incurvata* in particular, can be found growing as extensive circular mats on exposed alpine tundra outcrops. *Lescuraea saxicola* on the other hand, form smaller, more dense mats on rocks in alpine areas, and on mineral soil in areas of higher latitude. Saxicolous taxa are particularly abundant on seepage cliffs and seepage slopes in subalpine to alpine areas. As well, some taxa are epiphytic or terricolous. The epiphytic taxon *L. stenophylla* can be found growing on lower branches and twigs of bushes (*Alnus*, *Salix*, *Acer*, and *Chamaecyparis*) in subalpine areas, often near sources of water. *Lescuraea mutabilis*, endemic to Europe, is epiphytic on *Rhododendron* and *Fagus* Krummholz in alpine areas. Terricolous taxa, such as *L. radicosa* var. *denudata*, form extensive loose mats or wefts on soil under species of *Cassiope*, *Carex*, and Poaceae in alpine tundra and meadows.

2.5. Taxonomic Treatment of *Lescuraea* Bruch & Schimp. *in* B.S.G. in North America

The taxonomic treatment of *Lescuraea* includes the following: 1) Key to several taxa in the Leskeaceae, 2) Key to the infrageneric taxa of *Lescuraea*, 3) Key to the taxa of *Lescuraea*, and 3) Typified taxa, including current synonymy. Species are listed alphabetically within each infrageneric taxon. Infraspecific taxa of *Lescuraea* are presented in keys within the species complex.

2.5.1. Key to several taxa in the Leskeaceae

1. Laminal cells multipapillose on both surfaces 2
1. Laminal cells smooth or unipapillose on both surfaces 3

2. Leaves with costa single, ending mid-leaf or longer, pellucid; laminal cells with 2-5 (1) distinct papillae on lumen .... ***Claopodium*** (Lesq. & James.) Ren. & Card.
2. Leaves with costa short and double, ending well below or mid-leaf; laminal cells with multiple minute papillae over lumen .... ***Leptopterigynandrum austroalpinum***

3. Plants autoicous; annulus present; leaf margins entire and plane; costa single, subpercurrent or ending abruptly mid-leaf; laminal cells with a single papillae centred over cell lumen 4
3. Plants dioicous; annulus present or absent; leaf margins entire and plane, or acumen serrate and ± recurved throughout; costa variable, or single subpercurrent to percurrent, smooth throughout or distal abaxial surface prorate; laminal cells smooth, papillose, or prorate 5

4. Stems and branches with paraphyllia ± numerous; costa stout throughout, percurrent; laminal cells rounded-hexagonal; alar cells ± quadrate .... ***Leskea*** Hedw.
4. Stems and branches with paraphyllia absent; costa narrowing abruptly and ending ± mid-leaf; laminal cells hexagonal to short-rhombic; alar cells ± angular or transversely elliptic .... ***Lindbergia brachyptera***

5. Stem and branch leaves somewhat differentiated, not plicate below; leaf margins entire and plane throughout; costa variable, short and double, lacking, or single and diffusing out abruptly in acumen, smooth; stem central strand present; paraphyllia absent; laminal cells thick-walled, ± round or elongate, smooth; alar cells transversely elongate-elliptic; capsules narrowly cylindric, mostly > 2 mm long; annulus present ………………………………… ***Leskeella*** (Limpr.) Loeske. and ***Pseudoleskeella*** Kindb.
5. Stem and branch leaves similar, ± biplicate below; leaf margins serrate above and ± recurved throughout; costa single, stout, mostly subpercurrent to percurrent, distal abaxial region prorate; stem central strand present or absent; paraphyllia numerous or absent; laminal cells variable, isodiametric, elliptic, rhomboidal, fusiform-linear, to linear, thick- or distinctly thin-walled, not pitted or pits present; cells papillose or prorate; alar cells mostly quadrate, sometimes transversely elongate cells interspersed; capsules ± short cylindric to elongate-globose, < 1.0 to 2.0 mm long, rarely slightly longer; annulus absent ……………………………………………… 6

6. Plants large to very large; leaves with short or long hyaline hair point, smooth; costa stout below, narrowing out and ending well below the leaf apex, distal abaxial region scarcely prorate; stem central strand absent; paraphyllia absent; capsule ± globose-cylindric ……………………………………… ***Rigodiadelphus baileyi*** (p. 130)
6. Plants small to large; leaves acute to acuminate, never with hyaline hair point, serrate above; costa stout throughout, subpercurrent to percurrent, ± distinctly prorate in distal abaxial region; stem central strand present; paraphyllia mostly numerous; capsule cylindric ………………………… ***Lescuraea*** Bruch & Schimp. *in* B.S.G. (p. 42)

2.5.2. Key to the infrageneric taxa of *Lescuraea* Bruch & Schimp. *in* B.S.G.

1. Plants lustrous; laminal cells ± linear, thin-walled; proximal exostome surface with horizontal ridges, upper region with coarse and densely distributed papillae; endostome segments filiform, hyaline, cilia lacking…. subgenus *Lescuraea* (p. 45)
1. Plants ± dull; laminal cells isodiametric to elliptic-fusiform, thick-or thin-walled; proximal exostome surface papillose-striate, rarely striate, upper region with large and rounded, sparsely distributed papillae; endostome segments broad and

keeled, narrowly keeled, or terete, yellowish-hyaline or orange-brown, cilia filiform (2-3), broad and short (1-2), rudimentary or nearly lacking .... subgenus *Pseudoleskea* (p. 57)

2.5.3. Key to the taxa of *Lescuraea* Bruch & Schimp. *in* B.S.G.

1. Laminal cells with papillae centred or off-centre 2
1. Laminal cells with papillae over upper cell end (prorate) 3

2. Leaves ovate, short acuminate or acute; laminal cells ± isodiametric, thick-walled; distinct papillae centred over cell lumen of most cells (except alar and basal), off-centre in elongate cells; alar region medium (extending nearly ⅓ up leaf margin), cells ± quadrate, rigid; capsule ± arcuate, never erect; endostome segments yellowish, broad, distinctly keeled; basal membrane high (to ½ height of segments); cilia (1-3) filiform .... ***L. patens*** (p. 84)
2. Leaves lanceolate, very long acuminate, acumen longer than leaf proper; laminal cells ± rhomboidal-elongate, thin-walled; small papillae off-centred, limited to distal cells; alar region small (extending ≤ ¼ up leaf margin), cells enlarged-quadrate to elongate, lax; capsule erect; endostome segments orange-brown, narrow and ± terete; basal membrane low (≤ ¼ height of segments); cilia lacking or rudimentary vestiges present .... ***L. stenophylla*** (p. 121)

3. Laminal cells ± fusiform-linear to linear, strongly prorate throughout (except alar and basal); costa distinctly prorate in distal abaxial region; inner perichaetial leaves erect, linear-lanceolate, abruptly short or long acuminate, costa stout and percurrent; or perichaetial leaves spreading, broad and acute, costa weak and ending mid-leaf; endostomal basal membrane high or low (nearly ½ or ≤ ¼ height of segments); cilia filiform or lacking 4
3. Laminal cells rhomboidal-fusiform, fusiform-linear, or otherwise; distal and few median cells ± weakly prorate; costa indistinctly prorate above; inner perichaetial leaves erect, lanceolate, gradually ± long acuminate, costa ± stout below, weak above and ending in upper acumen or percurrent; endostomal basal membrane ± medium (to ⅓ height of segments); cilia broad and short or lacking 5

4. Laminal cells distinctly pitted throughout (except alar); inner perichaetial leaves linear-lanceolate, abruptly short acuminate, costa stout and percurrent; capsule arcuate and asymmetric; endostomal basal membrane high; cilia (1-2) filiform .... ***L. atricha*** (p. 60)

4. Basal cells only ± pitted; inner perichaetial leaves otherwise, costa stout and percurrent or weak and ending mid-leaf; capsule inclined or erect and symmetric; endostomal basal membrane low; cilia lacking 6

5. Leaf margins of acumen serrate to crenate, cells of margin short < 2: 1; laminal cells commonly ≤ 7.2 μm wide, variable in shape, irregular, elliptic, rhombic, and elongate, distinctly thick-walled, never pitted; distal cells sometimes strongly prorate; alar cells quadrate with numerous transversely elongate cells, mostly < 10 μm in length and width; paraphyllia never branched, cells ± isodiametric or round, thick-walled .... ***L. incurvata*** *sensu lato* (p. 68)

5. Leaf margins serrate to serrulate, cells of margin longer > 2: 1; laminal cells commonly 9.6-12.0 μm wide, homogeneous in shape, rhomboidal to fusiform-linear, thin-walled, slightly pseudo-pitted throughout (except alar); distal cells never strongly prorate; alar cells ± enlarged quadrate to elongate, mostly > 12 μm long and > 10 μm wide; paraphyllia somewhat to distinctly branched, cells quadrate-elongate, thin-walled .... ***L. radicosa*** *sensu lato* (p. 96)

6. Leaves abruptly long acuminate from a wide base; margins of acumen broadly recurved throughout; laminal cells never linear, often ± sinuose and thick-walled; median cells mostly < 24 μm long; alar region large (often extending ½ up leaf margin), cells ± quadrate; inner perichaetial leaves linear-lanceolate, abruptly long acuminate, costa stout and percurrent; endostome segments yellow-brown to orange, narrowly keeled or terete .... ***L. saviana*** (p. 115)

6. Leaves ovate-acute to acuminate; margins ± recurved throughout; laminal cells ± linear and thin-walled; median cells mostly > 24 μm long; alar region ± small, cells rarely extending ¼ up leaf margin, quadrate-elongate; inner perichaetial leaves broad and short acuminate, costa weak and ending mid-leaf; endostome segments hyaline and filiform (rudimentary) .... ***L. saxicola*** (p. 47)

2.5.4. Typified taxa

Lescuraea Bruch & Schimp. *in* B.S.G., Bryol. Eur. 5: 101 (fasc. 46-47. Monogr. 1).1851.

Type: *Lescuraea striata* (Hedw. *in* Schwägr.) Bruch & Schimp. *in* B.S.G.

Nomenclatural notes: Bruch and Schimper (1851) described *Lescuraea* to accommodate three taxa that display erect, symmetric, and cylindric capsules, as well as rudimentary peristomes. Based on protologue information, Bruch and Schimper (1851) clearly chose *Lescuraea striata* as the type of this genus.

Bruch and Schimper described *Pseudoleskea* a year later for two taxa with arcuate, asymmetric, cylindric capsules, and a peristome that is 'hypnalean' in nature. Unfortunately, type material of *Hypnum atrovirens* Brid. was unavailable on loan. However, Ignatov and Afonina (1992) place this name in synonymy with the older name *Leskea incurvata* Hedw. The lectotype of *Leskea incurvata* Hedw. at G along with several syntypes, were examined and clearly fit the description of *Hypnum atrovirens* Bridel.

In 1900, Best formally suggested *Lescuraea* (1851) and *Pseudoleskea* (1852) to be congeneric. As a result, Best (1900) accepted *Pseudoleskea* and recognised three subgenera within the genus for the placement of taxa, one of which (*Eu-Pseudoleskea*) was first created by Kindberg in 1897. On the other hand, Lawton (1957) kept the older name *Lescuraea*, and created three subgenera to accommodate all of the taxa (Table 2.1).

Based on a number of gametophytic as well as sporophytic characters that are unique to these two generic names within the Leskeaceae, it does not seem appropriate to separate them into two genera. Several sporophytic differences are attributed to reduction, as plants have become corticolous or saxicolous. Due to the similarities between taxa in both genera, the author agrees with both Best (1900) and Lawton (1957), in recognising *Lescuraea* and *Pseudoleskea* as congeneric. In the current revision, two subgenera of *Lescuraea* (*Lescuraea* and *Pseudoleskea*) are accepted.

Description: Plants small to large-sized, soft and lax, somewhat julaceous and robust, or stiff and robust, forming ± densely intertwining mats or very loose mats or wefts; yellowish, yellow-green, green, orange-green, to brown, older stems and branches yellow-orange to brown, very old stems devoid of leaves, brown and wiry, or brown and not devoid of leaves; dull, satin-glossy, to lustrous. Stems prostrate, apices slightly to distinctly hooked; distinctly to somewhat fragile when dry; outer cortical cells between 1-2 layers to 3 - 4 layers, orange-red, ± thick-walled; cells of medulla thin-walled, rounded, abruptly large-lumened, to somewhat thick-walled, angular, and gradually large-lumened, hyaline; central strand ± distinct. Branching irregularly; branches numerous to few or nearly lacking, short to long; prostrate or erect. Rhizoids smooth; orange-brown; numerous to nearly lacking; branching profusely or not at all branched; ± forming densely matted tufts along stems, matted tufts uncommon near stem apex. Paraphyllia multiform, filamentous and foliose; short to long filamentous, not at all to distinctly branched; cells thin-walled to distinctly thick-walled, quadrate, rounded-quadrate, rhomboidal to elongate, ± prorate or not at all prorate; numerous on younger portions of stems and branches, ± lacking on very old stems. Stem leaves loosely to densely arranged; erect and appressed to julaceous when dry, spreading or erect when moist; somewhat to distinctly concave below; symmetric to distinctly asymmetric, not or slightly falcate to distinctly falcate-secund; distinctly biplicate, sometimes numerous longitudinal plicae throughout; narrowly short or long decurrent; ovate and abruptly short acuminate to ovate-lanceolate and gradually long acuminate, acumen distinctly shorter or longer than the leaf proper; 0.65-2.38 mm long x 0.29-1.01 mm wide. Branch leaves similar in shape to stem leaves, usually somewhat smaller. Margins distinctly to slightly serrate at apex, acumen distinctly to slightly serrate; ± narrowly recurved from lower acumen to leaf base or narrowly recurved from lower acumen to mid-leaf, broadly recurved from mid-leaf to leaf base, sometimes more so on one side, not recurved from upper to lower acumen. Costa yellowish-green, green, to orangeish; subpercurrent, distinctly percurrent, or ending in lower acumen; stout below, narrowing in acumen; abaxial surface ± keeled; slightly to distinctly prorate along upper abaxial portion. Laminal cells echlorophyllose to chlorophyllose, translucent to opaque. Alar region small to large, usually extending from ¼ to ½ up leaf margin; cells thin-walled, lax, and enlarged quadrate to enlarged rectangular, to thick-walled, transversely-elongate or quadrate; 4.8-28.8 µm long x 4.8-16.8 µm wide. Basal cells thin-walled and lax to thick-walled; never pitted or slightly pitted cells in some; enlarged quadrate, quadrate, to rectangular; 7.2-48.0 µm long x 7.2-16.8 µm wide. Median cells thin-walled, pseudo-pitted, and mostly homogeneous throughout to thick-walled, not or distinctly pitted, and not or distinctly heterogeneous throughout; marginal cells smaller; 7.2-60.0 µm long x 3.6-12.0 µm wide. Distal cells similar to median; 7.2-57.6 µm long x 3.6-12.0 µm wide. Papillae round or rarely angled; on upper or central cell lumen to prorate; branch leaves more distinctly papillose or prorate. Dioicous. Perichaetia common to very rare; shiny and opaque to satin and translucent; inner perichaetial leaves broadly ovate-acuminate to linear-lanceolate, gradually or abruptly short to long acuminate, somewhat serrate above, squarrose to distinctly erect throughout; costa weak, narrow, and ending mid-leaf or lower acumen, to stout, ending in acumen or excurrent; basal cells lax, rectangular, and forming an oblique region from costa to leaf margin, median cells thin-walled, long fusiform-linear to linear, distal cells thin-walled, short-rhomboidal, fusiform, to linear; prorae lacking or present. Perigonia rare, sometimes several along stems, none seen on branches; perigonial bracts ovate-acuminate, appressed, concave, entire; costa narrow, ending mid-leaf or lacking; basal cells not or slightly lax, rectangular, median cells ± thin-walled, sinuose-fusiform; prorae lacking. Sporophyte rare to common. Seta smooth; yellow-orange, orange-red, to red; dextrorse below, sinistrorse above; 5.0-20.0 mm long. Capsule distinctly or slightly arcuate, suberect, or erect and cylindric; ± symmetric or symmetric; red-purple, red-brown, orange, orange-brown, or yellow-orange; rough and dull or smooth and lustrous; constricted below mouth when dry, mouth ± flaring outward or not constricted below mouth when dry; capsule swollen when moist; 0.5-2.0 mm long. Operculum conical to short rostrate. Peristome inserted along mouth or deeply inserted below mouth of capsule. Exostome teeth orange to yellow-orange below, yellowish to hyaline above; lanceolate and slightly 'shouldered' to nearly linear and not 'shouldered'; inflexed, distal portions touching endostome segments or straight; joined at base to form an orange-brown or yellow-orange band; proximal dorsal surface with fine horizontal striae, papillose-striae, or ridges from ¼ to ½ height of tooth, fine papillose-striae or fine papillae in vertical or oblique pattern in median portion, fine papillae leading to sparsely distributed, large and rounded papillae or densely distributed, small and coarse papillae in distal portion of tooth; apex sharp to distinctly blunt; ventral surface distinctly or slightly trabeculate; 200-500 µm long. Endostome segments yellowish and as long or somewhat shorter than exostome to hyaline and distinctly shorter than exostome; lanceolate, distinctly keeled and straight to linear, filiform and straight or somewhat inflexed above; narrowly or indistinctly perforate along median line; narrowly or widely spaced, joined to form a high, medium, or low basal membrane of similar colour ½ to ¼ height of segments; dorsal and ventral surfaces somewhat sparse and minutely papillose or dense and coarsely papillose throughout; 70-372 µm long; cilia filiform, reduced, or lacking. Spores minutely to coarsely papillose; 9.6-24.0 µm in diameter.

Habitat: *Lescuraea* is predominantly saxicolous on siliceous or rarely alkaline rocks, boulders, and outcrops, as well as corticolous, or terricolous. Specimens range in elevation from 250-3350 metres, in subalpine forests and alpine tundra.

Distribution: *Lescuraea* displays a Holarctic distribution in subalpine to alpine regions of Europe, northern, eastern, and western Asia and western North America. *Lescuraea* is disjunct in areas of higher relief in eastern North America. Examination of a number of taxa from Africa, South America, and the Himalayas revealed that they do not belong in *Lescuraea* (refer to Chapter 3 for a discussion on unconfirmed taxa).

Lescuraea* Bruch & Schimp. *in* B.S.G. subg. *Lescuraea

Type: *Lescuraea striata* (Hedw. *in* Schwägr.) Bruch & Schimp. *in* B.S.G.

Isothecium subg. *Lescuraea* (Bruch & Schimp. *in* B.S.G.) Boulay, Musc. France 142. 1884. **Type:** *Isothecium striatum* (Hedw. *in* Schwägr.) Spruce

Pseudoleskea subg. *Lescuraea* (Bruch & Schimp. *in* B.S.G.) Best, Bull. Torr. Bot. Cl. 27: 233. 1900. **Type:** *Pseudoleskea substriata* Best

Lescuraea* subg. *Eulescuraea* Broth. Nat. Pflanzenf. I (3): 997. 1907. *nom. illeg. incl. typ. gen.* **Type: *Lescuraea striata* (Hedw. *in* Schwägr.) Bruch & Schimp. *in* B.S.G.

Nomenclatural notes: Boulay (1884) considered *Lescuraea* a subgenus of *Isothecium* (Brachytheciaceae). Then Best (1900) recognised *Lescuraea* as a subgenus of *Pseudoleskea*. Lastly, Lawton (1957) devised three subgenera of *Lescuraea*, and the following taxa were placed within subgenus *Lescuraea*: *L. striata*, *L. saxicola*, and *L. iliamniana*.

According to Crosby *et al.* (1999), there are nine valid species in the genus *Lescuraea sensu stricto* worldwide. Of these, only one (*Lescuraea saxicola*) is also found in North America. *Lescuraea striata* (= *L. mutabilis*), which has often been confused with *L. saxicola*, is an epiphytic taxon from Europe.

After having examined type material of several other taxa listed by Crosby *et al.* (1999), I determined that these taxa do not belong in *Lescuraea* (Table 2.5). I follow Lawton (1957) in reassigning *Lescuraea arizonae* (Williams) P.S. Wilson & Norris to *Pseudoleskeella*. Type material of *L. chilensis* Herz. (from Chile) and *L. serrata* Warnst. (from Europe), were determined to be *Amblystegium tenax* var. *spinifolium* (Schimp.) Jenn. and *Eurhynchium praelongum* (Hedw.) Bruch & Schimp. *in* B.S.G., respectively.

Both *Lescuraea darjeelingensis* Vohra and *L. secunda* Arnell have been treated in a revision and are listed as 'well known' taxa by Crosby *et al.* (1999). However, only *L. darjeelingensis* Vohra was made available on loan, and it clearly does not belong in *Lescuraea*. Conversely, *Lescuraea glacialis* Amann and *L. longipes* Broth. & Par. are listed as 'poorly known' taxa (Crosby *et al.* 1999). Unfortunately, type material of neither species was not received on loan. Consequently, their status cannot be verified.

Description: Plants small to medium-sized, sometimes very small, soft and lax; yellow to yellow-green, with orange tinges; distinctly lustrous. Paraphyllia numerous to very few on stems and branches, sometimes nearly lacking; cells thin-walled. Costa ± orange tinged; ± stout throughout; ending well before apex or somewhat subpercurrent. Laminal cells distinctly echlorophyllose and translucent; homogeneous throughout, fusiform-linear to distinctly linear; cells thin-walled. Alar region small to medium, rarely extending ¼ up leaf margin; cells thin-walled, somewhat lax, enlarged quadrate to elongate. Papillae round; prorate. Perichaetia rare; shiny and opaque; inner perichaetial leaves broadly ovate-lanceolate, abruptly acuminate to a short point; clasping seta below, progressively spreading above, distinctly squarrose above; costa very weak, narrow, ending mid-leaf or below. Sporophyte occasional. Seta thin; yellow-orange to orange.

Capsule erect, cylindric, symmetric; yellow-orange to red-brown; somewhat smooth and shiny, rarely rough and dull; not or rarely slightly constricted below mouth when dry, mouth not flaring outward. Peristome deeply inserted below mouth of capsule, rudimentary. Exostome teeth yellow-orange below, hyaline above; linear, gradually acuminate, rarely slightly 'shouldered' at base; proximal dorsal surface with horizontal ridges from ¼ or sometimes nearly ⅓ height of tooth, vertically or obliquely papillose striate in median portion, small, coarse and densely distributed papillae in distal portion of tooth; apex mostly blunt; ventral surface indistinctly trabeculate, minutely papillose throughout. Endostome segments hyaline; distinctly shorter than exostome; filiform or slightly terete, never keeled; straight or slightly inflexed at apex; not or slightly slit along median line; widely spaced, joined to form a low basal membrane of similar colour to nearly ¼ height of segments; dorsal and ventral surfaces large, coarse, and densely papillose throughout, rarely somewhat minutely papillose; cilia lacking, never vestigial protuberances between segments. Spores somewhat large and coarsely papillose; 14.4-22.0 µm in diameter, mostly 16.8-21.6 µm in diameter.

Lescuraea saxicola (Bruch & Schimp. *in* B.S.G.) Molendo, Moostud. 144, 147, 149. 1864. Figure 2.16-2.18

Lescuraea striata β. Saxicola Bruch & Schimp. *in* B.S.G., Bryol. Eur.5: 103. Pl. 459: β (fasc. 46-47. Mon. 2.). 1851. **Type:** "var. β In Saxis umbrosis Alpium" **Neotype – NY** (not seen)

Ptychodium decipiens Limpr., Die Laubm. 2: 799. 1895.

Type: "Steiermark: Neualm bei Schladming 1700-1900 m cfrct. (Breidler 30. August 1877), Patzenkar bei Schladming 1800 m (Breidler 18. August 1870), Seckauer Zinken 2200 m, Krahbergzinken bei Schladming 2100 m und Krautkareck in den Kraggauer Alpen 2520 m (sämtlich von J. Breidler entdeckt); Kärnten: Hühnerberger Alpe bei Gmünd 2500 m (Breidler 20. August 1881); Tirol: Langtauferer Ochsenalm im Ober-Vintschgau 2700 m (Breidler 6. August 1882); Tatra: am Grossen Fischsee (Limpricht am 2. August 1873)." **Lectotype – BP !** (*Breidler* 30. August 1877, lectotypus); **syntype – BP !** (*Limpricht* 2. August 1873)

Pseudoleskea decipiens (Limpr.) Kindb., Bull. Soc. Bot. Ital. 1896: 17. 1896.

Lescuraea frigida Kindb., Eur. & N.Am. Bryin. 26. 1896.

Type: "*Amer.* r. Can. Northern Labrador: Macoun 1896."

Holotype – S (not seen)**; isotype – WTU!**

Pseudoleskea substriata Best, Bull. Torr. Bot. Cl. 27: 233. 8f. 17-24. 1900.

Type: "British Columbia; type in coll. of Geol. Surv. of Canada; collected by Prof. John Macoun on rocks below Hector, Rocky Mts., Aug. 13. 1890. R.S. Williams, rocks on shores of Lake Lindeman, Northwest Territory, May 21, 1898. Sterile." [*Williams 557*] **Holotype – CANM** (*Macoun*, not seen)**; isotypes – NY !, WTU !, MO !, F !; paratypes –** (*Williams 557*) **NY !, FH !,US !**

Lescuraea substriata (Best) Paris, Ind. Bryol. ed. 2. 3: 159. 1905.

Lescuraea mutabilis var. *saxicola* (Bruch & Schimp. *in* B.S.G.) Hagen, Kgl. Norske Vidensk. Selsk. Skr. 1908 (9): 53. 1909.

Lescuraea decipiens (Limpr.) Loeske, Hedwigia 50: 312. 1911.

Lescuraea julacea Besch. & Card. *in* Card., Bull. Soc. Bot. Genéve ser 2, 3: 284. 1911. **Type:** "Japon: Ganju (n. 14480, sér. I; Uyematsu, herb. Brotherus); Hayachine (n. 14374, sér I; n. 3233; Ubayu (n. 2813)." (annotation: as *Lescurœa julacœ*) **Lectotype – PC !** (*Faurie 14480*, lectotypus)**; syntype – H-BR !** (*Faurie 3233*)

Pseudoleskea striata var. *saxicola* (Bruch & Schimp. *in* B.S.G.) Dix. *in* Dix.& James., Brit. Mosses, ed. 2. 423. 1924.

Lescuraea mutabilis var. *decipiens* (Limpr.) Mönkem., Die Laubm. Eur. 692. 1927.

Lescuraea frigida subsp. *substriata* (Best) Grout, Checklist Pleuroc. Moss. N. Am. 25. 1929.

Pseudoleskea frigida (Kindb.) Sharp *in* Grout, Moss Fl. N.Am. 3: 190. 1934.

Brachythecium perrevolutum Broth. *ex* Ihsiba, Bot. Mag. 49: 600. 1935.

Fide Iwatsuki, 1991. **Type:** "Hab. Mt. Togakusi, Sinano. (ISHIBA)" [Japan, Nipponicæ] **Holotype – H-BR** (not seen)

Ishibaea julacea (Besch. & Card. *in* Card.) Toyama, Act. Phytotax. Geobot. 7:

264. 1938. *Fide* Iwatsuki, 1991.

Lescuraea iliamniana E. Lawton, Bull. Torr. Bot. Cl. 84: 349. 1957.

Type: "Alaska, Thomas s.n. (LAWTON)." [Alaska, Iliamna Bay, southeast of Anchorage, on rock, *Rhoda Thomas*, Sept. 5, 1952 (LAWTON)]

Holotype – WTU !

Pseudoleskea iliamniana (E. Lawton) Crum, Steere, & Anderson, The Bryologist 67: 163. 1964.

Pseudoleskea saxicola (Bruch & Schimp. *in* B.S.G.) Crum, Steere, & Anderson, The Bryologist 67: 164. 1964.

Pseudoleskea julacea (Besch. & Card.) Crum, Steere, & Anderson, The Bryologist 76: 103. 1973.

Nomenclatural notes: In Bruch, Schimper, and Gümbel's Bryologia Europaea II, Bruch and Schimper (1851) described *Lescuraea striata β saxicola*, giving only a general locality "In Saxis umbrosis Alpium." Unfortunately, neither a collector nor a collection number was provided. Specimens received from BM do not correspond with the minimal type information. A single specimen has the name *Lescuraea striata* var. *β saxicola*. However, the handwriting on the packet clearly indicates the collector and date as Breidler, 1875. The other specimens indicate *Isothecium striatum* var. *rupincola* or *Anomodon sriatus* var. *saxicola*. The former was collected in 1839 and the latter has no collection date, though it is a later described (1861) name. There is no indication Bruch or Schimper even viewed any of these specimens. Due to minimal information from both the protologue and the BM material, I do not feel confident in choosing a type at BM. As a last resort, Gümbel's herbarium at TUB was also searched. Unfortunately, no specimens were available. Lawton (1957) also indicated that she had not seen the type, pointing out that it was from the "European Alps without definite locality." As a result, Lawton (1957) selected *Molendo 63* at NY as a neotype. This specimen has not been received on loan.

Limpricht described *Ptychodium decipiens* in 1895 from specimens collected by Breidler and Limpricht in the Alps and in the Polish Carpathians. From the available syntype material received, Breidler's specimen (*Ptychodium decipiens n. sp.*, cfrct, 30.

August 1877) at BP is chosen here as the lectotype. The other available type specimen at BP (also *Ptychodium decipiens n. sp.*) collected by Limpricht, is cited here as a syntype. The remaining syntype material listed in the type citation was not received from BP. Consequently, it is unknown if the material at BP still exists or simply was not provided on loan. Lawton (1957) indicated that she could not receive Limpricht's type material for *P. decipiens*. However, based on Limpricht's description, Lawton was able to place *P. decipiens* in synonymy with *Lescuraea saxicola*.

Lescuraea frigida was described by Kindberg in 1896 from a specimen collected by Macoun in northern Labrador. The holotype was not received from S. However, a specimen at WTU is chosen as an isotype. The packet at WTU contains a label clearly indicating that it is a portion of a specimen from Kindberg's herbarium (as *n. sp.*) in the Naturhistoriska Riksmuseum in Stockholm. Lawton (1957) indicated that type material of *L. frigida* at S-PA, was collected by A.P. Low on July 31, 1896. However, this does not correspond with the protologue. Unfortunately, no material from S-PA was received to verify Lawton's claim.

Best described *Pseudoleskea substriata* in 1900 from specimens collected by Macoun in the Rocky Mountains of British Columbia, and by Williams in the Northwest Territory. In the type citation, Best clearly indicated that Macoun's specimen is the type, and that it is in the 'collection of the Geological Survey of Canada'; which has since been incorporated into CANM. Best was conscientious in identifying type material, writing 'type' or 'portion of type' on packet labels. This is evident on packets of other new species that G. N. Best described in 1900. The holotype of *P. substriata* at CANM has not been studied. However, it should have the word 'type' clearly written on the packet label. Specimens of Macoun at NY, WTU, MO, and F, lack the word 'type' on packet labels. However, all other information matches the type citation. These specimens are clearly synonymous with *Lescuraea saxicola* and are cited as isotypes. Williams' specimens at NY, FH, and US are cited as paratypes.

Bescherelle and Cardot described *Lescuraea julacea* in 1911 from Japanese specimens collected by Faurie. From the limited syntype material received, *Faurie 14480* at PC is chosen here as the lectotype. The specimen at H-BR, *Faurie 3233*, is cited here as a syntype. It seems clear that both specimens, along with the others listed in the type citation, were used to describe the new species. Although both specimens are sterile and otherwise equal, the former is chosen as the lectotype since the name on the packet matches the newly described name, and is from Cardot's herbarium at PC. The latter specimen, although formerly from the herbarium of Cardot and now in Brotherus' herbarium at H, does not seem to indicate that this is a new species but rather a variety, var. *julacea*, of *Lescuraea striata*. It is unknown whether the other syntype material still exists, or simply was not provided on loan. Noguchi (1972) placed *L. julacea* in synonymy with *L. saxicola*, which was supported by Noguchi *et al.* (1991) as well as the current revision.

According to Iwatsuki (1991), *Brachythecium perrevolutum*, described by Brotherus *ex* Ihsiba in 1935, is synonymous with *Lescuraea saxicola*. The type specimen from H has not been examined.

Lawton described the holotype of *Lescuraea iliamniana* at WTU in 1957 for an Alaskan specimen collected by Rhoda Thomas. Then in 1965 Lawton placed *L. iliamniana* in synonymy with *L. saxicola*, and personal observations support this judgement.

Description: Plants small to medium-sized, sometimes very small, soft and lax, forming dense or somewhat loosely intertwining mats; yellow to yellow-green, with orange tinges, sometimes green, older stems and branches distinctly brown; distinctly lustrous. Stems prostrate, thin, apices distinctly or rarely somewhat hooked; somewhat to distinctly round when dry or moist; fragile when both dry or moist; outer cortical cells of 2-3 layers, orange to orange-red, thick-walled; cells of medulla somewhat thin-walled, angular, gradually large-lumened, hyaline; central strand distinct. Branching irregularly, branches numerous, often longer than stems, 2° and 3° branches numerous, prostrate or erect. Rhizoids smooth; red-brown; occasional; not branching; forming tufts along stems; rarely few along branches. Paraphyllia multiform, filamentous to lanceolate-foliose; cells thin-walled, rhomboidal-elongate, fusiform, or rectangular; numerous to very few on stems and branches, sometimes nearly lacking. Stem leaves densely arranged; somewhat julaceous to erect and appressed when dry, patent to spreading when moist; acumen short or rarely somewhat long and erect; ± distinctly concave below; asymmetric, distinctly or somewhat falcate; distinctly biplicate; short or narrowly long decurrent; ovate and abruptly short acuminate, short pointed, or blunt apex, to lanceolate and gradually acuminate; acumen distinctly shorter or rarely as long as leaf the proper; 0.75-1.32 mm long x 0.22-0.60 mm wide, mostly 1.05-1.22 mm long x 0.39-0.53 mm wide. Branch leaves similar in shape to stem leaves, usually somewhat smaller; somewhat to distinctly serrate at apex. Margins distinctly to somewhat serrate at apex, acumen serrate to somewhat entire; broadly recurved from upper or middle acumen to leaf base. Costa ± orange tinged; ending well before apex, rarely somewhat subpercurrent; stout below, remaining stout above or rarely becoming narrower in lower acumen; abaxial surface distinctly or rarely only slightly keeled; distinctly prorate along upper abaxial portion. Laminal cells distinctly echlorophyllose, translucent. Alar region medium to small, usually extending well below ¼ up leaf margin; cells thin-walled, somewhat lax; quadrate to elongate; 4.8-21.6 µm long x 4.8-9.6 µm wide, mostly 7.2-14.4 µm long x 7.2-9.6 µm wide (rarely to 21.6 µm long). Basal cells somewhat to distinctly thick-walled, not lax; often distinctly or somewhat pitted; short-rectangular to oblong-linear; 9.6-45.6 µm long x 7.2-12.0 µm wide, mostly 16.8-33.6 µm long x 9.6 µm wide (rarely to 45.6 µm long). Median cells thin-walled; homogeneous throughout; fusiform-linear to distinctly linear, sometimes cell ends rounded; 14.4-52.8 µm long x 3.6-7.2 µm wide, mostly 24.0-36.0 µm long x 4.8 µm wide (rarely less than 24.0 µm or greater than 40.8 µm long). Distal cells thin-walled; fusiform to oblong-linear; 7.2-45.6 µm long x 3.6-7.2 µm wide, mostly 19.2-36.0 µm long x 4.8 µm wide (rarely greater than 38.4 µm long). Papillae round; prorate; limited to some median and most distal cells; stem leaves distinctly or rarely only somewhat prorate; branch leaves more distinctly prorate; common on dorsal and ventral leaf surfaces. Perichaetia rare, shiny and opaque; perichaetial leaves broadly ovate-lanceolate, abruptly acuminate to a short point, slightly to indistinctly serrate above; clasping seta below, progressively spreading above, distinctly squarrose when moist; costa very weak, narrow, ending mid-leaf or below, rarely slightly above mid-leaf; basal cells slightly or not lax, rectangular, distal and median cells thin-walled, distinctly linear, rarely slightly fusiform; prorae lacking. Perigonia rare, limited to several along stems; none seen along branches; perigonial bracts ovate, acute, appressed, concave, entire to slightly serrate at apex; costa single and ending mid-leaf, short and double and ending near base, or lacking; basal cells lax, fusiform, distal and median cells somewhat thin-walled, fusiform-linear, somewhat vermicular; prorae lacking. Sporophyte occasional. Seta smooth, thin; yellow-orange to orange; straight or slightly dextrorse below, distinctly sinistrorse above; 4.5-16.5 mm long. Capsule erect, cylindric, symmetric; yellow-orange to red-brown; somewhat smooth and shiny, rarely rough and dull; not or rarely slightly constricted below mouth when dry, mouth not flaring outward, swollen when moist; 1.0-1.9 m long. Operculum short rostrate, slightly oblique. Peristome deeply inserted below mouth of capsule, rudimentary. Exostome teeth yellow-orange below, hyaline above; linear, gradually acuminate, rarely somewhat 'shouldered' at base; slightly inflexed above, distal portions not touching endostome segments; adhering somewhat to endostomal membrane; joined at base to form a yellow-orange or orange-brown band; proximal dorsal surface with horizontal ridges from ¼ or sometimes nearly ⅓ height of tooth, vertically or obliquely papillose striate in median portion, dense and coarsely papillose in distal portion of tooth; apex blunt, rarely somewhat sharp; ventral surface slightly trabeculate, papillose throughout; 200-320 µm long. Endostome segments hyaline; distinctly shorter than exostome; filiform, not keeled, straight or slightly inflexed at apex; not perforate along median line; widely spaced, joined to form a low basal membrane of similar colour to nearly ¼ height of segments; dorsal and ventral surfaces densely and coarsely papillose throughout, rarely somewhat minutely papillose; 70-180 µm long; cilia lacking, no vestigial protuberances between segments. Spores somewhat coarsely papillose; 14.4.0-22.0 µm in diameter, mostly 16.8-21.6 µm in diameter. N = 9 (Fritsch 1982).

Diagnostic characters: *Lescuraea saxicola* has ovate-acuminate or sometimes lanceolate, asymmetric and shiny leaves that are abruptly short or rarely gradually acuminate. This taxon has fusiform-linear basal cells that are often somewhat to distinctly pitted throughout. However, median and distal cells are linear and never pitted. Prorae are abundant on most distal and some median cells. Paraphyllia are numerous in some specimens and nearly lacking in others. The perichaetium, which is shiny and opaque, is similar to that of *Rigodiadelphus baileyi* in that the inner perichaetial leaves are broadly ovate-lanceolate and spread outward. In addition, the costa of the inner perichaetial leaf is distinctly weak and ends mid-leaf or below. The capsule is erect, cylindric, symmetric, and somewhat shiny. The exostome teeth are linear-lancoelate, vertically or obliquely striate or papillose striate, and coarsely papillose from a somewhat broadened, horizontally ridged base. However, round perforations or holes between the joints (as in *L. mutabilis*) are lacking. The endostome segments are filiform, dense and coarsely papillose throughout, and joined to form a low basal membrane. The spores are somewhat large and coarsely papillose. This taxon is found predominantly on siliceous rocks and boulders in forests and alpine meadows, and on mineral soil at high latitudes.

Lescuraea saxicola has often been confused with *L. mutabilis*, the former initially described by Bruch & Schimper (1851) as a variety of the latter. Even recently, specimens identified as *L. mutabilis* are mounted on herbarium sheets with *L. saxicola*, and identified with the name of the latter taxon. Gametophytically they are quite similar. Where *L. mutabilis* has long lanceolate leaves, *L. saxicola* has ovate-acuminate, ovate-lanceolate, or sometimes long lanceolate leaves. Paraphyllia may be few or numerous in *L. saxicola*. However, the filamentous forms are never branched, as in *L. mutabilis*. The perichaetia between the two species are also quite distinct. Where *L. mutabilis* has lanceolate, satin, and translucent, clasping perichaetial leaves, *L. saxicola* has broadly ovate-lanceolate, shiny and opaque clasping leaves, with a large proportion of the leaf distinctly spreading when dry to nearly squarrose when moist. The perichaetial leaf costa is stout, percurrent to distinctly excurrent in *L. mutabilis*, and weak, narrow, and ending mid-leaf in *L. saxicola*. As indicated earlier, the perichaetium described in *L. saxicola* is similar to that of *Rigodiadelphus baileyi* (see the discussion on *R. baileyi* for diagnostic characters between the two).

Two sporophytic characters help differentiate *Lescuraea mutabilis* from *L. saxicola*. First, the horizontally ridged proximal portion of the tooth in *L. mutabilis* is low and slightly 'shouldered'. This ridged base terminates abruptly whereby the remainder of the tooth is narrow, linear, and densely and coarsely papillose throughout. Second, the median line that extends through the coarsely papillose portion of the exostome of *L. mutabilis* is always distinctly punctured or perforated, forming a row of single holes in between the joints along the height of the tooth. In *L. saxicola*, the distinction between the proximal and median portion of the tooth is somewhat more gradual, with the horizontal ridges leading to fine papillae in the median portion, and coarse papillae in the distal portion of the tooth. In addition, the exostome of *L. saxicola* is never punctured or perforated by holes along the median line. No other species in *Lescuraea* in North America can be mistaken for either *L. mutabilis* or *L. saxicola.*

Variation: Leaf length and width varies from 0.75-1.32 mm long x 0.22-0.60 mm wide (usually 1.05-1.22 mm long x 0.39-0.53 mm wide), both within and between specimens. Leaf shape also varies considerably, with most specimens having ovate-acuminate leaves. However, lanceolate leaves are not uncommon, especially in more sheltered specimens. Specimens from Japan and Alaska tend to have more lanceolate leaves and few paraphyllia, whereas most European, eastern, and most western North American specimens tend to have ovate-acuminate leaves and abundant paraphyllia. *Lescuraea julacea* tends to have more lanceolate leaves as well as fewer paraphyllia or paraphyllia nearly lacking. These character states do not support recognition of *L. julacea* as a distinct species. As such, *L. julacea* has been placed in synonymy here. Several European and North American specimens (excluding Alaska) of *L. saxicola* also revealed more lanceolate leaves with few to no paraphyllia present along stems and branches.

Sporophytically, all of the specimens are extremely similar, with some variation only in the ornamentation and extent of the 2° cell wall deposition on the outer peristomial layer. The ornamentation and extent of this deposition (e.g., ridges, papillose-striae) on the OPL surface is variable, with some teeth having ridges to nearly ⅓ the height of the tooth, while others have minimal deposition with the ridges barely reaching ¼ the height of the tooth. This variation can be found both within a single exostome as well as between specimens. The ornamentation of the exostome above that of the ridges is either striate or papillose striate, and gradually leads to the coarse papillae above. The endostome and spores may be dense and coarsely papillose or sparse and finely papillose, although most tend to be that of the former. Often the peristome is deeply inserted below the mouth of the capsule such that very little of the 2° cell wall material on the exostome is visible.

Habitat: *Lescuraea saxicola* occurs on dry granite, quartzite rocks, and boulders in forests and meadows, as well as on rock outcrops and sandstone cliffs in or near sources of seepage in alpine areas. At high latitudes, this species is common on mineral soil at lower elevations. It is rarely found on limestone rocks or cliffs. Elevation: approximately 250-3325 metres, mostly from 1000-3000 m.

Distribution: *Lescuraea saxicola* is not common in North America. In western North America, it has been collected from Attu Island and some localities on mainland Alaska; one locality in the Yukon Territory; central and southern British Columbia, including the Queen Charlotte Islands; and a few localities in Washington, Colorado, and Utah. This species is disjunct in eastern North America from Mt. Mansfield in Vermont; Gaspé, Lac Guillaume-Delise, and Nitchequon in Quebec; Labrador; and Gros Morne in Newfoundland. This species has also been reported from several districts in Greenland, including the Skjoldungen district. This species is more common in Scandinavia, Europe, and in Russia. Several specimens have been collected from Kazakhstan, China, India, and Japan.

Specimens examined: ASIA: CHINA: Xinjiang: Fukang Co.: S. end of Lake Tian-chi – *Tan 93-840* (FH). **KAZAKHSTAN:** Alma-Ata Oblast – *Allen 10810* (COLO); Leninogorsk – *Bryantseva 2046* (MO); Tian Shan Mountains – *Lisowski* (F). **JAPAN: Ganju:** *Faurie 14480* (PC – lectotype). **Hayachine:** *Faurie 3233* (H-BR 2333 014 – syntype). **Hokkaido:** Ishikari Prov.: Mt. Ashibetsu – *Schofield, Iwatsuki & Yoshimura 46206* (UBC); Mt. Sapporo – *Ando* Aug. 6, 1958 (UBC). **Honshu:** Nagano – *Iwatsuki 1011* (UBC). **INDIA: Kashmir:** Nichinai Valley – *Townsend 87/313* (COLO). **EUROPE: Alps** – in herb. *Thomas* (BM). Reistad – *Ryan* Juli 1886 (F). **ARMENIA:** Caucasus Mountains – *Vašák* (COLO). **AUSTRIA:** Kärnten – *Froehlich* Aug. 2, 1949 (UBC). Steiermark – *Breidler* 30. August 1877 (BP – lectotype). Secthaler bei Lindenburg – *Breidler* 23. Juli 1875 (BM). **FINLAND:** Utsjoki – *Hult* Aug. 14, 1880 (UBC). **FRANCE:** Isére, les Deux Alpes – *DeSloover 34.886, 34.937* (DUKE). **GERMANY:** Rhöngebietes – *unknown collector* anno 1839 (BM). **NORWAY:** Oppland: Vågå – *Størmer* July 26, 1952 (UBC). Horre: near the Breifond Hotel – *Nicholson 79* (UBC). **POLAND:** Tatra – *Limpricht* Aug. 2, 1873 (BP – syntypes (2 specimens)). **RUSSIA:** Kola Peninsula, Chibiny Mountains: Murmansk (COLO). **Sweden:** Jämtland: Bomsund – *Åberg* Sept. 13, 1913 (UBC). **TURKEY:** Kuzey Anadolu Daglari Mountains: Mt. Ardanuç – *Davis & Hedge 30404*

(COLO). Taurus Mountains: Adana distr., Bahçe (COLO). **North America: Canada: Alberta:** Banff National Park: Lake Louise – *Crum & Schofield 5341* (WTU). **British Columbia:** Omineca Mtns: Peak Range: Mt. Hartley – *Ireland & Bellolio-Trucco 18679* (F). Rocky Mountains: Hector – *Macoun* Aug. 13, 1890 (isotypes –NY, F, MO, WTU), Wilmore Wilderness Area: Hardscrabble Pass – *Krieger 1779* (ALTA). North Vancouver: Mt. Seymour – *Schofield 15944* (DUKE) *31095* (UBC). Queen Charlotte Islands: Moresby Island – *Schofield 31095* (UBC). Selkirk Mtns: B.C. Forestry Alpine Recreation Area: Meadow Mtn – *Tan & Teng 78-484* (UBC). Wilmer District: below lake of Hanging Glaciers – *MacFadden 4058, 1084* (WTU). **Labrador:** Twin Falls Area: Scotts Falls – *Brassard 6415* (MICH). Head of Kangalaksiorvik fiord – *Weber 1558* (ALTA). English Point Area – *Belland & Piercey 4177* (UBC). **Quebec:** Lac Guillaume-Delise: U. of Laval base camp – *Ireland 21272* (DUKE), *Ireland 21362* (F). Gaspé: Tabletop Mtn – *Collins 4411-A* (MICH). **Yukon:** Lake Lindeman – *Williams 557* (paratypes – NY, FH, US), *Williams 157* (UBC). **Greenland:** Skjoldungen District: Siiiorartussoq – *Lewinsky* (ALTA). **USA: Alaska:** Aleutian Islands: Attu Island – *Howard 708, 720* (US). Ambler River Region – *Lewis 2413* (F). Central Pacific Coast District: Valdez Quadrangle – *Hermann 21716* (UBC, US), Iliamna Bay – *Thomas* Sept. 5, 1952 (WTU – holotype). Mt. Eilson (Copper Mtn) – *Weber & Viereck 10096* (COLO). **Colorado:** Mineral Co.: San Juan National Forest: Westfork Campground – *Schofield & Jamieson 83334* (DUKE). San Juan Co.: b/w main Highway and Lime Creek Road – *Griffin 264* (DUKE). **Utah:** Dagget Co.: Uintah Mtns: Spirit Lake – *Flowers 8197* (WTU). Duchesne Co.: Uintah Mtns: Ottoson basin – *Flowers 9628* (COLO). **Vermont:** Mt. Mansfield – *Lorenz 37* (WTU, FH). **Washington:** Kittitas Co.: Lower Keechelus Valley – *Bailey July 1916* (MO). Mt. Baker – *Spence 2265* (UBC).

Lescuraea Bruch & Schimp. *in* B.S.G. **subg. *Pseudoleskea*** E. Lawton, Bull. Torr. Bot. Cl. 84(4): 286. 1957.

Pseudoleskea Bruch & Schimp. *in* B.S.G., Bryol. Eur. 5: 147 (fasc. 49-51. Monogr. 1). 1852. **Type:** *Pseudoleskea atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G.

Hypnum sect. *Pseudoleskea* (Bruch & Schimp. *in* B.S.G.) Hampe, Flora 50: 78.

1867.

Leskea sect. *Pseudoleskea* (Bruch & Schimp. *in* B.S.G.) Mitt., Jour. Linn. Soc. Bot. 12: 567. 1869.

Hypnum subg. *Pseudoleskea* (Bruch & Schimp. *in* B.S.G.) Lesq. & James, Man. Mosses N. Am. 317, 319. 1884.

Pseudoleskea* subg. *Eu-Pseudoleskea* Kindb., European and North American Bryineae (Mosses) 1: 49. 1897. *nom. illeg. incl. typ. gen.* **Type: *Pseudoleskea atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G.

Pseudoleskea subg. *Radicosella* Best, Bulletin of the Torrey Botanical Club 27(5): 228. 1900. **Type:** *Pseudoleskea radicosa* (Mitt.) Lesq. & James. (lectotypus).

Pseudoleskea* sect. *Eu-Pseudoleskea* Broth., Die Natürlichen Pflanzenfamilien I (3): 1000. 1907. *nom. illeg. incl. typ. gen.* **Type: *Pseudoleskea atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G.

Nomenclatural notes: In the past, *Pseudoleskea* has been considered a section of *Hypnum* and of *Leskea* and finally a subgenus of *Hypnum* in 1884. In 1897, Kindberg devised two subgenera *Eu-Pseudoleskea* and *Ptychodium* to accommodate 17 taxa in North America, while in 1900 Best provided three subgenera within *Pseudoleskea*, two of which (*Eu-Pseudoleskea* and *Radicosella*) are synonymous with subgenus *Pseudoleskea*. Shortly thereafter, Brotherus (1907) incorporated the two subgenera *Eu-Pseudoleskea* and *Radicosella* into section *Eu-Pseudoleskea*. Lastly, in 1957 Lawton considered *Pseudoleskea* to be a subgenus of *Lescuraea*, including in this subgenus all taxa known to occur in Europe and North America, except those in subgenera *Lescuraea* and *Tricholeskea* (Table 2.1).

After multiple requests, protologue information for *Hypnum atrovirens* Brid. (= *Lescuraea incurvata*) was unavailable, and as such, type material was not reviewed. Ignatov and Afonina (1992) consider *Pseudoleskea atrovirens* (Dicks. *ex* Brid.) Schimp. synonymous with *L. incurvata*. Type material of *Leskea incurvata* Hedw. was reviewed. According to Crosby *et al.* (1999) there are 31 valid species in *Pseudoleskea* worldwide. Of these, eight are found in North America. Having examined type material of a number of taxa listed by Crosby *et al.* (1999), the following conclusions are made. Of the eight taxa, six are placed in subgenus *Pseudoleskea*, *P. baileyi* is transferred to *Rigodiadelphus*, and *P. julacea* (Besch. & Card.) Crum, Steere, and Anderson and *P. brachyclados* (Schwägr. *in* Schultes) Kindb., are placed in synonymy with *Lescuraea saxicola* and *L. radicosa*, respectively. Of the remaining 23 taxa, three are identical and considered to belong to *Pseudoleskeella* or *Leskeella*, and four taxa are identified as not belonging in the Leskeaceae (Table 2.5). Consequently, 16 taxa were unavailable for study, and thus insufficiently known.

Description: Plants small to large-sized, soft and lax to julaceous and robust; yellow-green, green, orange-green, green-brown, or brown-black; dull. Paraphyllia numerous along stems and branches; cells thin or thick-walled. Costa green, yellow-green, to orange-tinged; ± stout throughout, ending abruptly in mid-acumen to distinctly percurrent. Laminal cells chlorophyllose and opaque to ± echlorophyllose and ± translucent; homogeneous to distinctly heterogeneous throughout, rhomboidal, elliptic-fusiform, elongate, elliptic, or isodiametric and angular. Alar region small, medium, to large, extending from ¼ to nearly ½ up leaf margin; cells thin-walled and lax or thick-walled, enlarged elongate, quadrate, to transversely elongate. Papillae round; on upper or centre of lumen to prorate. Perichaetia occasional to common; satin and translucent; inner perichaetial leaves ovate-lanceolate to linear-lanceolate, gradually long and slenderly acuminate to abruptly short or long acuminate or apiculate; erect and clasping seta throughout; costa ± stout, ending in lower acumen to extending into apiculate acumen. Sporophyte occasional to common. Seta thicker; yellow-orange, orange, to red. Capsule arcuate, suberect, to erect and cylindric; asymmetric to rarely somewhat symmetric; orange to red-brown; distinctly rough and dull; constricted below mouth when dry, mouth ± flaring outward. Peristome inserted along mouth of capsule. Exostome teeth yellowish-orange below, yellow-hyaline above; lanceolate, somewhat 'shouldered'; inflexed to incurved, distal portions touching endostome segments; joined at base to form an orange-brown band; proximal dorsal surface with fine horizontal striae or papillose-striae from ¼ to nearly ½ height of tooth, fine papillose-striae or papillae in vertical, oblique, or circular pattern in median portion, large, rounded, and sparsely distributed papillae in distal portion of tooth; apex sharp to somewhat blunt; ventral surface distinctly trabeculate. Endostome segments yellowish to orange-brown; as long or longer than exostome; lanceolate, distinctly keeled or terete, straight or rarely slightly inflexed at apex; broad or narrowly gaping along median line; narrowly or widely spaced, joined to form a high, medium, or rarely low basal membrane of similar colour nearly ½ or rarely as low as ¼ height of segments; dorsal and ventral surfaces somewhat sparse and minutely papillose throughout. Cilia long filiform (1-3), medium and stub-like, or with rudimentary vestiges. Spores minutely papillose; variable, 9.6-21.6 µm in diameter, mostly 9.6-18 µm in diameter.

Subgenus *Pseudoleskea*: 6 species

- *L. atricha* (Kindb.) E. Lawton
- *L. incurvata* (Hedw.) E. Lawton
    - *L. incurvata* (Hedw.) E. Lawton var. *incurvata*
    - *L. incurvata* var. *gigantea* E. Lawton
    - *L. incurvata* var. *tenuiretis* (Culm.) E. Lawton
- *L. patens* (Lindb.) Arn. & C. Jens.
- *L. radicosa* (Mitt.) Mönkem.
    - *L. radicosa* (Mitt.) Mönkem. var. *radicosa*
    - *L. radicosa* var. *compacta* (Best) E. Lawton
    - *L. radicosa* var. *denudata* (Kindb.) E. Lawton
- *L. saviana* (DeNot.) E. Lawton
- *L. stenophylla* (Ren. & Card.) Kindb.

Lescuraea atricha (Kindb. *in* Macoun) E. Lawton, Bull. Torr. Bot. Cl. 84: 306. 60-65. 1957. Figure 2.19-2.21

Pseudoleskea atrovirens var. *atricha* Kindb. *in* Macoun, Cat. Canad. Pl. Part VI, Musci. 6: 180. 1892. **Type:** "On rocks along the Eagle River, just below the bridge at Griffin Lake, B.C., August 13, 1889. (*Macoun*)" **Lectotype – S !** (lectotypus); **isotypes – S !** (2 specimens), **NY !**

Pseudoleskea atricha (Kindb.) Kindb., Ottawa Naturalist 7: 20. 1893.

Nomenclatural notes: *Pseudoleskea atrovirens* var. *atricha* was described by Kindberg in Macoun's (1892) Catalogue of Canadian Plants, from specimens collected by Macoun in 1889. Lawton (1957) indicated that she reviewed the holotype from S, although I could see no indication of her having done so. There are three packets in S loosely affixed to a single herbarium sheet, with label information corresponding to the type citation. The middle packet contains a large specimen, as well as a hand-written label with some locality information, a clear collection number, and date. Although the handwritten collection date on the packet as August 12, 1889 does not match exactly with the date in the type citation, this specimen is chosen as the lectotype. The upper packet also contains a large specimen, although the hand-written label within the packet contains less information. The locality is merely listed as 'Canada' and the substrate as 'rocks'. A collection number of '332' appears to have been crossed out and '335' written in its place. However, a small slip of paper also included in the packet has the date '1891' and the collection number of '332'. This specimen is designated as an isotype. Lastly, the lowermost packet contains a small portion of the type, which is designated as an isotype.

Lawton (1957) indicated that isotypes are at NY and US, although no type material was seen at US. There is a slide at NY that also matches the type citation, and is designated as an isotype.

Description: Plants small to medium-sized, tumid, and somewhat robust, forming densely intertwining mats; yellow-green, orange-green, to black, older stems and branches distinctly orange-black; dull. Stems prostrate, apices not or somewhat hooked; round or somewhat elliptic when dry, round when moist; somewhat to distinctly fragile when dry; outer cortical cells of 2-3 layers, orange-red, thick-walled; cells of medulla ± thin-walled, angular, gradually large-lumened, yellowish-hyaline; central strand distinct. Branching irregularly, branches numerous, 2° to 3° branches abundant, usually short and prostrate. Rhizoids smooth; orange-brown; occasional; not or branching slightly; forming tufts along stems and branches; loose, matted tufts more common near stem apex. Paraphyllia multiform, filamentous to foliose, mostly filamentous; unbranched; cells thick-walled, quadrate to slightly elongate, often somewhat prorate; numerous on stems and branches. Stem leaves densely arranged; tumid to julaceous and appressed when dry, erect or spreading when moist, the short acumen incurved; distinctly concave throughout; asymmetric, rarely slightly falcate; distinctly biplicate, numerous; narrowly short decurrent; ovate and abruptly acuminate to a short point, sometimes more gradually acuminate; the acumen distinctly shorter or rarely almost as long as the leaf proper; 0.83-1.35 mm long x 0.33-0.92 mm wide, mostly 1.01-1.25 m long x 0.34-0.65 mm wide. Branch leaves similar in shape and size to stem leaves, more distinctly serrate above. Margins distinctly serrate at apex, acumen distinctly serrate; broadly recurved from lower acumen to leaf base, rarely somewhat recurved from upper to lower acumen, sometimes more distinctly recurved on one side. Costa orange-tinged; subpercurrent to percurrent; stout below, narrowing slightly above, somewhat to distinctly flexuose in acumen; abaxial surface keeled; distinctly prorate along upper abaxial portion. Laminal cells mostly chlorophyllose and opaque. Alar region medium, extending ¼ to ⅓ up leaf margin; cells ± thick-walled, some lax cells interspersed; quadrate to short-elongate, sometimes transverse-elongate cells interspersed; 4.8-16.8 µm long x 7.2-12.0 µm wide, mostly 7.2-12.0 µm long x 7.2-9.6 µm wide (rarely from 14.4-16.8 µm long). Basal cells thick-walled; somewhat to distinctly pitted throughout; short-rectangular to somewhat elongate, often quadrate cells interspersed; 9.6-43.2 µm long x 4.8-9.6 µm wide, mostly 14.4-24.0 µm long x 7.2 µm wide (rarely from 26.4-40.8 µm long). Median cells thick-walled, distinctly pitted throughout, rarely indistinctly pitted; somewhat differentiated from costa to leaf margin, fusiform to fusiform-linear with rounded ends near costa, rarely smaller cells interspersed, becoming smaller towards leaf margin; 12.0-48.0 µm long x 3.6-7.2 µm wide, mostly 19.2-33.6 µm long x 4.8 µm wide (rarely from 40.8-45.6 µm long). Distal cells thick-walled, somewhat to distinctly pitted throughout; somewhat fusiform-linear below, becoming rhomboidal above; 12.0-43.2 µm long x 3.6-7.2 µm wide, mostly 16.8-28.8 µm long x 4.8-7.2 µm wide (rarely greater than 31.2 µm long). Papillae round; prorate; median and distal cells distinctly prorate, alar cells slightly prorate; branch leaves more distinctly prorate; prorae common on abaxial and adaxial leaf surfaces. Perichaetia rare, satin and translucent; inner perichaetial leaves erect, linear-lanceolate, abruptly acuminate to a short point, acumen distinctly serrate; clasping seta throughout; costa stout and percurrent; basal cells lax, rectangular, median cells thick-walled, occasionally somewhat pitted, fusiform-linear, distal cells thick-walled, rarely somewhat pitted, short-rhomboidal to fusiform, somewhat prorate. Perigonia rare, limited to few along stems, none seen on branches; perigonial bracts ovate-acuminate, appressed, concave, entire, apex sometimes cucullate; costa lacking; basal and median cells lax, oblong to long-fusiform, distal cells thick-walled, short-fusiform, prorae lacking. Sporophyte rare. Seta smooth; red to red-brown, becoming orange-red when old; straight or somewhat dextrorse below, distinctly sinistrorse above, 5.5-12.0 mm long. Capsule arcuate or rarely suberect, cylindric, asymmetric; red-orange to red-brown; somewhat rough and dull; constricted below mouth when dry, mouth flaring outward, swollen when moist; 0.5-1.3 mm long. Operculum conical, sometimes with a minute nipple or apiculus. Peristome inserted below mouth of capsule. Exostome teeth yellowish-orange below, yellow-hyaline above; lanceolate, somewhat 'shouldered'; inflexed, rarely distinctly incurved, distal portions touching endostome segments; joined at base to form a yellow or yellow-orange band; proximal dorsal surface with fine horizontal striae to nearly ½ height of tooth, obliquely striate in median portion, fine papillae leading to sparse and rounded papillae in distal portion of tooth; apex somewhat blunt; ventral surface distinctly trabeculate; 370-425 µm long. Endostome segments yellowish to yellow-hyaline, sometimes somewhat yellowish-orange; as long or longer than exostome, sometimes broken off; lanceolate, distinctly keeled, straight; narrow to broadly perforate along median line; narrowly spaced, joined to form a medium to high basal membrane of similar colour ⅓ to nearly ½ height of segments; dorsal and ventral surfaces sparse and minutely papillose throughout; 243-424 µm long; cilia linear, 1-2, sometimes broken off at base, appendiculate. Spores minutely papillose, 9.6-19.2 µm in diameter, mostly 14.4-18.0 µm in diameter. N = not reported.

Diagnostic characters: *Lescuraea atricha* is endemic to western North America, and is characterised by julaceous and stiff, somewhat robust plants that predominantly inhabit exposed rock outcrops. This species has asymmetric, ovate leaves that gradually end in a short or rarely somewhat long point. The acumen is distinctly shorter or rarely as long as the leaf proper. The laminal cells (except alar) are mostly thick-walled and distinctly pitted throughout. Other than *Rigodiadelphus baileyi*, no other taxon in *Lescuraea* has pitted laminal cells. *Lescuraea saxicola* often has pitted basal cells; yet, median and distal cells are never pitted. *Lescuraea atricha* can be easily distinguished from *R. baileyi* in that it never exhibits a hyaline hair point. Stems and branches in *L. atricha* are mostly round when dry or moist, and have central strands as well as paraphyllia. The costa is stout, percurrent and distinctly prorate above, and the capsule is arcuate and cylindric, never globose cylindric as in *R. baileyi* (see distinguishing characters for *R. baileyi*).

Sporophytically, *Lescuraea atricha* is similar to other taxa such as *L. incurvata* and *L. patens*. No significant distinguishing characters are present.

Variation: Most of the variation in *Lescuraea atricha* is in leaf length and width, 0.83-1.35 mm long x 0.33-0.92 mm wide (mostly 1.01-1.25 m long x 0.34-0.65 mm wide), with the shape and size of the laminal cells somewhat variable, yet homogeneous within specimens. Most plants are julaceous and somewhat robust, with sporophytes rare. Capsules are mostly arcuate; however, suberect capsules do sometimes occur.

Habitat: *Lescuraea atricha* occurs predominantly on rocks and rock outcrops in subalpine *Tsuga-Picea* forests, as well as on exposed ridges in alpine areas. However, it is not exclusive to these forest types. This species occasionally grows on soil near boulders, rock outcrops and cliff faces. Elevation: approximately 671-2290 metres (mostly 1525-2300 m, rarely less than 900 or greater than 2300 m).

Distribution: *Lescuraea atricha* has been collected from northwestern and southwestern British Columbia, including Vancouver Island; as well as the northwestern portion of Washington. Single collections were made in northeastern Washington, the Central Pacific Coast District, and in the Alexander Archipelago in Alaska.

Specimens examined: NORTH AMERICA: CANADA: British Columbia: Cassiar District: Omineca Mtns: Peak Range – *Ireland & Bellolio-Trucco 18870* (MO). Monashee Mts: Gold Range – *Macoun 385* (S – lectotype, S – isotypes (2 specimens)). Mt.Brackenridge – *Boas* anno 1966 (UBC). Northern B.C.: Three Guardsmen Pass – *Worley 12280* (UC/JEPS). Vancouver Island: Strathcona Provincial Park: E. side of Buttle Lake – *Krieger & Hebben 1858, 1859, 1860, 1861* (ALTA), *Spence & Scagel 1916*(UBC), Mt.

Albert Edward – *Price & Halbert 6427* (UBC); Mt. Arrowsmith – *Halbert 3989a* (UBC). Whistler Mtn – *Schofield 37902* (UBC), *Van Velzen & Leong 302.80609* (UBC). **USA: Alaska:** Aleutian Islands: Adak Island – *Jordal & Miller 3258* (MICH). Alexander Archipelago: Baranof Island – *Worley & Boas 10124* (UBC). Central Pacific Coast District: Valdez – *Hermann 21612* (MICH). **Washington:** Clallam Co.: Bogachiel Mtn – *Eyerdam 3639* (DUKE). Jefferson Co.: Olympic Mtns – *Frye 546* (WTU). Lewis Co.: Mt. Ranier National Park: Mt. Rainier – *Lawton 4994* (WTU), *Foster 336* (FH, MO). Pacific Co.: along Nehmah River – *Anderson 14799* (DUKE). Pend' Oreille: near Gypsy Lake – *Layser 1085* (WTU). Pierce Co.: S. slope Mt. Rainier – *Hermann 18568* (MICH). Snohomish Co.: Mt. Pilchuk – *Lawton 4553* (WTU). Whatcom Co.: Mt. Baker National Forest – *Sutherland 1130* (WTU), *Vanderspek & Ralph 60-1030B* (WTU).

Lescuraea incurvata (Hedw.) E. Lawton, Bull. Torrey Bot. Cl. 84: 290. 1957. Figures 2.22-2.26

Leskea incurvata Hedw., Sp. Musc. 216. 53 f. 8-14. 1801.

Type: "*Locus*. Haud infrequens in montanis regionibus; eg. supra lapides Novosae summitatis Sudetem." [Pfarrkuppe, Ludwig] **Lectotype – G !; syntypes – G !** (6 specimens)

Hypnum atrovirens Dicks. *ex* Brid., Musc. Recent. 2(2): 153. 1801. *Fide* Ignatov & Afonina 1992. **Type:** "In Scotia, Guiana et Patagonia in Sylnis ad arbores habitat." **Syntypes –** (not seen)

Hypnum attenuatum Dicks. *ex* With., Syst. Arr. Brit. Pl. ed. 4, 3: 342. 1801. *Fide* Wijk *et al.* 1964. **Type:** protologue unavailable

Hypnum filamentosum Dicks. *ex* With., Syst. Arr. Brit. Pl. ed. 4, 3: 845. 1801. *Fide* Wijk *et al.* 1964. **Type:** protologue unavailable

Hypnum implexum Brid., Musc. Recentiorum 2(2): 150. 4 f.3. 1801.

Type: "In Alpium Allobrogicarum Helveticarumque paludofis, caespitibus implexis laete crescens, fed femper absque fructu inueni; hinc Florescentiae tempus incertum. Duratio perennis." **Lectotype – B !** (lectotypus)

Leskea incurvata var. *implexa* (Brid.) Brid., Musc. Recent. Suppl. 2: 81. 1812.

Pseudoleskea atrovirens (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G., Bryol. Eur. fasc. 49-51. 1852.

Lescuraea filamentosa (Dicks. *ex* With.) Lindb., Musci Skand. 36. 1879.

Pseudoleskea atrovirens var. *filamentosa* (Dicks. *ex* With.) Boul., Muscin. France 162. 1884.

Lescuraea atrovirens (Dicks. *ex* With.) Kindb., Rev. Bryol. 12: 29. 1885.

Pseudoleskea filamentosa (Dicks. *ex* With.) C.Jens., Medd. Groenland. 3: 341. 1887.

Pseudoleskea oligoclada Kindb. *in* Macoun, Bull. Torrey Bot. Cl. 17: 277. 1890. **Type:** "On damp rocks, Mount Benson, Nanaimo, Vancouver Island, June 8, 1887." [*Macoun*] **Holotype – S !; isotypes – S !** (2 specimens)

Pseudoleskea falcicuspis C. Müll. & Kindb. *in* Macoun & Kindb., Cat. Can. Pl., Part VI, Musci: 182. 1892. **Type**: "On rocks, west side of Lake Mara, Sicamous, B.C., July 3rd, 1889; on rocks at the Illicillewaet Cañon, near Revelstoke, also at Quesnel, B.C. (*Macoun.*)." [Canadian Musci No.510] **Lectotype – S** (not seen)**; syntypes – COLO !, FH !** (3 specimens), **MICH !** (2 specimens), **UC/JEPS !, US !** (2 specimens)

Pseudoleskea incurvata (Hedw.) Loeske, Hedwigia 50: 313. 1911.

Nomenclatural notes: Hedwig described *Leskea incurvata* in 1801 for specimens collected by Ludwig on 'Pfarrkuppe', the mountainous region between former Czechoslovakia and Silesia, Germany. Geissler and Hedenäs (1999) lectotypified this species, along with many others in the Hedwig-Schwägrichen herbarium at G. The lectotype is affixed to a large herbarium sheet with six syntypes, and matches exactly with Figure 8 of table 53, in Hedwig's protologue (Fig. 2.23).

Lawton (1957) was unable to obtain Hedwig's type specimen for whatever reason, and chose to neotypify a specimen at NY (Germany: Silesia, Schneegrube, Riesengebirge, Limpricht, Bryoth. Sil. Oct. 1866, 78). Since Hedwig's type specimen is indeed available, the neotype is not retained.

Syntype material of *Hypnum atrovirens*, described by Dickson *ex* Bridel (1801), has not been received on loan. Ignatov & Afonina (1992) place this name in synonymy with *Pseudoleskea atrovirens* (Dicks. *ex* With.) Schimp. (= *Lescuraea incurvata* (Hedw.) Loeske).

The protologues of *Hypnum attenuatum* Dicks. *ex* With. and *Hypnum filamentosum* Dicks. *ex* With. after repeated attempts, were unavailable from any source. As such, the type citations are incomplete and type material has not been examined. Wijk *et al.* (1964) consider both names synonymous with *Lescuraea incurvata*.

Type material of *Hypnum implexum* Brid. at B has been examined, and is clearly synonymous with *Lescuraea incurvata*. However, the type specimen is somewhat more difficult to ascertain since the type locality identified by Bridel, as well as packet information, are somewhat vague. To complicate matters Bridel does not indicate a collector, collection number, or a collection date in the protologue. After having examined all of the specimens on the seven sheets received from B, it became obvious that the specimen Bridel used for Figure 3 in Table 4 of his protologue was not among the type material available from B. As a result, only specimens on sheets 0043/2001-4 and 0043/2201-5 could be considered possible type material, since they were labelled as *Hypnum implexum* and corresponded to the date of publication. The following specimen on sheet 0043/2001-5 from B is chosen as the lectotype (Fig. 2.24). This material is sterile and labelled as *H. implexum* 'In Alpium paludosis', which corresponds to the protologue. The collection date of 1796 also supports the selection of this specimen, since collection occurred before the publication date of 1801. It is also evident that Bridel later annotated the specimen. The remaining specimens on both sheets either have sporophytes, or were collected and included after the date of publication.

Type material of Kindberg's *Pseudoleskea oligoclada* Kindb. *in* Macoun is at S. In the protologue, Kindberg indicated that both capsules and male plants are unknown, and that Cardot believed this plant to be a variety of *Pseudoleskea atrovirens*. Of the three specimens affixed to the herbarium sheet, the uppermost specimen contains a label that matches the type citation, and is here designated as the holotype. The other two specimens are clearly small portions of the type and are here designated as isotypes. Wijk *et al.* (1967) also consider *Pseudoleskea oligoclada* synonymous with *Lescuraea incurvata*.

Type material of *Pseudoleskea falcicuspis* C. Müll. & Kindb. *in* Macoun & Kindb., has not been received from S. Syntypes examined from COLO, FH, MICH, UC/JEPS, and US are clearly synonymous with *Lescuraea incurvata*. In the type citation, Müller and Kindberg (1892) list three different localities in British Columbia, which is unusual. Looking at other species they described in the same publication, Müller and Kindberg only ever list one locality, as well as a collector and collection date. However, in the type citation for *Pseudoleskea falcicuspis* the first locality listed 'Lake Mara, Sicamous, B.C.' has a collection date, while the latter two localities do not. All of the specimens from the herbaria listed above are of the second locality 'on rocks at the mouth of the Illicillewaet Canyon, near Revelstoke, B.C.'. The labels on these packets all indicate 'Canadian Musci No. 510', the collection date as May 18, 1890, and the species name with 'N.Sp.' in parentheses. It is unclear whether Müller and Kindberg only intended specimens from the first locality to be the type, or from all three localities, thereby representing syntypes. It is unusual that the collection date is clearly written on the packet, yet Müller and Kindberg did not include it in the citation. However, as Müller and Kindberg did not designate the first specimen as the sole type, specimens from all three localities are to be considered syntypes.

***Lescuraea incurvata sensu lato*:**

Plants small to large-sized, julaceous and robust, forming ± dense to very loosely intertwining mats; yellow-green, green, orange-green, green-brown, to brown-black, older stems and branches distinctly orange to orange-brown; dull. Stems prostrate, apices ± distinctly hooked; elliptic when dry, round when moist; slightly to not fragile when dry or moist; outer cortical cells of 3 (4) layers, orange-red, thick-walled; cells of medulla ± thin-walled, angular, gradually large-lumened, hyaline; central strand distinct. Branching irregularly; branches few to abundant, branches usually short and somewhat erect; 2° branches few to numerous. Rhizoids smooth; orange-brown; occasional; not or branching slightly; forming tufts along stems; matted tufts common near stem apex of large plants; not along branches. Paraphyllia multiform, filamentous to lanceolate-foliose, unbranched; cells thick-walled, quadrate, rounded-quadrate, to slightly elongate; numerous on younger portions of stems and branches. Stem leaves ± loosely to densely arranged; tumid to ± julaceous and appressed to erect and appressed when dry, erect to spreading when moist; acumen short and incurved to long, flexuose and spreading; distinctly concave throughout or ± concave below; asymmetric, ± falcate to distinctly falcate-secund; distinctly to slightly biplicate; narrowly short or long decurrent; ovate and abruptly short acuminate, mostly to a short point or a blunt apex, to ovate-lanceolate, gradually acuminate to a long point; the acumen distinctly shorter or longer than the leaf proper, often somewhat falcate and twisted; 0.75-2.50 mm long x 0.38-0.93 mm wide, mostly 0.85-2.00 mm long x 0.52-0.80 mm wide. Branch leaves similar in shape to stem leaves, usually smaller, more distinctly serrate above. Margins distinctly serrate, crenate, or ± entire at apex, acumen distinctly serrate, ± crenate, to somewhat entire; broadly recurved from middle acumen to leaf base to narrowly recurved from lower acumen to leaf base with plain sections, sometimes recurved on one side only. Costa orange-tinged; ending abruptly in mid-acumen or distinctly percurrent; stout below, narrowing only slightly in acumen; abaxial surface distinctly keeled; distinctly to not prorate along upper abaxial portion. Laminal cells chlorophyllose to ± echlorophyllose, opaque to ± translucent. Alar region medium to ± large, usually extending ⅓ up leaf margin; cells thick-walled, not lax; transversely elongate, quadrate and very few elongate cells interspersed; 4.8-19.2 μm long x 7.2-12.0 μm wide, mostly 7.2-9.6 μm long x 7.2-9.6 μm wide (rarely from 14.4-19.2 μm long). Basal cells thick-walled, not lax or some cells slightly lax; not pitted; quadrate, short rectangular, to oblong-rectangular; 4.8-48.0 μm long x 4.8-12.0 μm wide, mostly 9.6-24.0 μm long x 7.2-9.6 μm wide (rarely from 19.2-48.0 μm long). Median cells very thick-walled; heterogeneous within leaf, many small and irregular to longer cells interspersed, marginal cells smaller; isodiametric and angular, short-rhomboidal, elliptic, elliptic-fusiform, to elongate; 4.8-40.8 μm long x 4.8-7.2 μm wide, mostly 7.2-24.0 μm long x 7.2 μm wide (rarely from 24.0-40.8 μm long). Distal cells thick-walled; short oblong to short rhomboidal; 4.8-31.2 μm long x 4.8-9.6 μm wide, mostly 7.2-19.2 μm long x 7.2 μm wide (rarely from 21.6-31.2 μm long). Papillae angular to round; prorate; limited to median and distal cells; stem leaves distinctly to slightly prorate, rarely prorae lacking; branch leaves more distinctly prorate, especially distal cells, reaching some median cells; common on dorsal and ventral leaf surfaces. Perichaetia occasional to common, satin and translucent; perichaetial leaves erect, ovate-lanceolate, gradually long and slenderly acuminate to distinctly apiculate, distinctly to ± serrate above; clasping seta throughout, long slender awn-like acumen occasionally spreading somewhat; costa ± stout below, ± narrower above, extending into lower acumen to ± percurrent, rarely ending mid-leaf to ± excurrent; basal cells lax, rectangular, median cells thick-walled, fusiform-linear to long rhomboidal, distal cells thick-walled, short-rhomboidal; somewhat prorate. Perigonia occasional, rarely one to several perigonia along stems, none seen on branches; perigonial bracts ovate-acuminate, appressed, concave, entire; costa narrow, ending in lower acumen; basal cells lax, fusiform-rectangular, median cells thin-walled, long-fusiform to rectangular, distal cells thick-walled, short-fusiform to short-rhomboidal; prorae lacking. Sporophyte occasional. Seta smooth; yellow-orange, orange, to red; straight to slightly destrorse below, distinctly sinistrorse above; 7.0-15.0 mm long. Capsule arcuate to suberect, cylindric, asymmetric; orange to red-brown; distinctly rough and dull; constricted below mouth when dry, ± mouth flaring outward, swollen when moist; 1.0-2.5 mm long. Operculum conic. Peristome inserted along mouth of capsule. Exostome teeth yellowish-orange below, yellow-hyaline above; lanceolate, somewhat 'shouldered'; inflexed, distal portions touching endostome segments; joined at base to form an orange-brown band; proximal dorsal surface with fine horizontal papillose-striae to nearly ½ height of tooth, sometimes finely striate in part, fine papillose-striae or papillae in vertical, oblique, or circular pattern in median portion, fine papillae leading to coarsely papillose in distal portion of tooth; apex sharp to somewhat blunt; ventral surface distinctly trabeculate; 317-480 µm long. Endostome segments yellowish-hyaline; as long or longer than exostome, rarely broken off; lanceolate, distinctly keeled, straight; narrowly perforate along median line; narrowly spaced, joined to form a medium basal membrane of similar colour ¼ to ⅓ height of segments; dorsal and ventral surfaces somewhat sparse and minutely papillose throughout; 223-470 µm long; cilia linear, 1-2, often broken off. Spores minutely papillose; variable, 9.6-21.6 µm in diameter, mostly 12.0-19.2 µm in diameter.

Variation: *Lescuraea incurvata sensu lato* is considerably variable in western North America. However there are distinct substrate and habitat driven character states that can be identified. Plants growing on exposed, dry, limestone boulders and outcrops, as well as on other alkaline substrates, tend to be small yet robust in appearance, as well as distinctly julaceous and compact. Laminal cells of these compact plants are isodiametric, angular, and the lumen extends into the prorae. The costa is stout and ends abruptly as an acute point in the lower to mid acumen. Somewhat less or equally exposed, slightly mesic to dry siliceous boulders and outcrops, tend to have somewhat robust small to medium plants that are slightly julaceous and less compact. Laminal cells of these plants are more elliptic and rounded. The cell is not seen to extend into the prorae, but rather prorae are round and distinct over the cell end. The costa is stout and narrows in the acumen, and is distinctly subpercurrent to somewhat percurrent. Lastly, plants that grow on soil over diffusely lit boulders, often in mesic conditions and surrounded by other bryophytes, tend to be large or even very large and robust, with distinctly falcate-secund leaves. These plants have laminal cells mostly elliptic and rounded, and prorae are often indistinct or nearly lacking. The costa is stout, narrows gradually above, and is distinctly percurrent.

Leaf length ranges from 0.78 to distinctly 2.50 mm long. The shortest leaves are asymmetric and distinctly incurved. Short to somewhat longer leaves are incurved and the acumen is often somewhat erect and twisted above. Long leaves are asymmetric, somewhat concave below, distinctly falcate-secund, and the long acumen is somewhat flexuose and spreading. Leaf width ranges from 0.38 to distinctly 0.93 mm wide. Shorter leaves tend to be more broadly recurved, as well as generally recurved from the lower acumen to the leaf base.

Key to the Infraspecific Taxa of *L. incurvata*

1. Plants large to very large, very robust; leaves mostly 1.70-2.00 mm long x 0.53-0.80 mm wide, distinctly ovate-lanceolate, long acuminate, acumen distinctly or rarely only somewhat longer than leaf proper; distinctly falcate-secund; laminal cells distinctly elliptic and rounded to elongate, or rarely somewhat rounded rhomboidal; prorae indistinct and few; predominant at lower elevations on mesic soil over boulders, often among other bryophytes .... ***L.incurvata* var. *gigantea*** (p. 76)
1. Plants small to medium, robust to somewhat robust; leaves mostly 0.84-1.40 mm long x 0.43-0.75 mm wide, distinctly ovate to somewhat ovate-lanceolate, short acuminate,

acumen distinctly to somewhat shorter than leaf proper; julaceous; laminal cells isodiametric and angular or rounded elliptic to elongate; prorae distinct and numerous; predominant at mid to high elevations on alkaline or siliceous rocks, boulders and outcrops 2

2. Plants small, robust; leaves mostly 0.84-1.10 mm long x 0.43-0.66 mm wide, distinctly ovate, short acuminate, acumen distinctly shorter than leaf proper; julaceous; laminal cells isodiametric and angular; cell lumina extending obliquely into prorae; mostly on alkaline rocks .... ***L. incurvata* var. *tenuiretis*** (p. 80)
2. Plants mostly medium, somewhat robust; leaves mostly 1.10-1.40 mm long x 0.52-0.75 mm wide, somewhat ovate to ovate-lanceolate, short to rarely somewhat long acuminate, acumen distinctly to somewhat shorter than leaf proper; somewhat julaceous, mainly incurved below, becoming erect and somewhat twisted above; laminal cells mostly rounded elliptic; prorae distinct, cell lumen not extending obliquely into prorae; mostly on siliceous rocks .. ***L. incurvata* var. *incurvata*** (p. 72)

Lescuraea incurvata* (Hedw.) E. Lawton var. *incurvata

Description: Plants small to medium-sized, julaceous and ± robust, forming ± densely intertwining mats; yellow-green to green, older stems and branches distinctly orange to orange-brown, dull. Stem apices distinctly hooked; fragile when dry; outer cortical cells of 2-3 layers. Branching: branches ± numerous, 2° branches few to numerous, often erect. Rhizoids branching slightly; matted tufts uncommon near stem apex. Stem leaves ± densely arranged; julaceous and appressed when dry, the short to somewhat long acumen slightly erect, spreading, and twisted; concave throughout; asymmetric, not falcate-secund; distinctly biplicate; narrowly and ± short decurrent; ovate to ± ovate-lanceolate, abruptly acuminate to a short or ± long apex, the acumen somewhat to distinctly shorter than the leaf proper; 0.88-1.48 mm long x 0.49-0.93 mm wide, mostly 1.10-1.40 mm long x 0.52-0.75 mm wide. Margins of acumen distinctly serrate to crenate; broadly recurved from middle acumen to base of leaf, sometimes more so on one side. Costa ending in upper acumen to ± percurrent; stout below, narrowing only slightly in acumen; distinctly prorate along upper abaxial portion. Laminal cells ±

chlorophyllose, ± opaque to translucent. Alar cells 4.8-19.2 µm long x 7.2-14.4 µm wide, mostly 7.2-12.0 µm long x 9.6-12.0 µm wide (rarely from 14.4-19.2 µm long). Basal cells thick-walled, some cells slightly lax; short rectangular to rectangular, some quadrate cells interspersed; 4.8-48.0 µm long, mostly 12.0-24.0 µm long x 7.2-12.0 µm wide (rarely from 31.2-48.0 µm long). Median cells highly variable, short elliptic, short-fusiform, short-rhomboidal, to elongate, with many small and irregular and longer cells interspersed; 4.8-40.8 µm long x 4.8-12.0 µm wide, mostly 9.6-24.0 µm long (rarely from 24.0-40.8 µm long). Distal cells 4.8-31.2 µm long x 4.8-9.6 µm wide, mostly 9.6-19.2 µm long (rarely from 21.6-31.2 µm long). Papillae round; prorate; distal cells of stem leaves distinctly prorate, median cells distinctly to somewhat prorate; branch leaves highly prorate. Perichaetia common. Sporophyte common. Seta yellow-orange to orange; 7.0-14.5 mm long. Capsule 1.0-2.0 mm long. Exostome teeth 312-460 µm long. Endostome segments 261-470 µm long. Spores 9.6-26.4 µm in diameter, mostly 12.0-19.2 µm in diameter. N = 9 (Kumar *et al.* 1988).

Diagnostic characters: *Lescuraea incurvata* var. *incurvata* is distinguished by: 1) its julaceous but not 'compact' plant habit; 2) ovate and abruptly acuminate to somewhat ovate-lanceolate leaves; 3) leaves incurved, with the acumen somewhat erect and slightly twisted; 4) an acumen slightly to distinctly shorter than the leaf proper; 4) distinctly prorate distal cells, leading to some median cells; and 5) predominantly saxicolous on siliceous rocks, boulders, and outcrops.

Lescuraea incurvata var. *incurvata* is distinctly intermediate between var. *tenuiretis* and var. *gigantea* in most of its character states, as well as being the most common. The same trend of 'compact', 'intermediate', and 'large' plants also occurs in *Lescuraea radicosa sensu lato*. Although the range in leaf and laminal cell sizes of *L. incurvata* var. *incurvata* does overlap with the upper and lower leaf and laminal cell sizes of var. *tenuiretis* and var. *gigantea* respectively, leaf shape including the attributes of the acumen, are limited mostly to this variety.

Variation: Most of the variation in *Lescuraea incurvata* var. *incurvata* is in leaf length and width, 0.88-1.48 mm long x 0.49-0.93 mm wide (usually 1.10-1.40 mm long x 0.52-0.75 mm wide), with the shape and size of the laminal cells highly variable and heterogeneous. However, heterogeneous laminal cells are typical for *Lescuraea incurvata sensu lato*.

Habitat: *Lescuraea incurvata* var. *incurvata* occurs on mesic or dry siliceous boulders and outcrops in forests, often near streams or other water sources; as well as forming extensive mats on siliceous outcrops in subalpine meadows and alpine tundra. It is rarely found on soil or on limestone. Elevation: approximately 900-3250 metres (mostly 1200-3000 m, occasionally less than 900 m). *Lescuraea incurvata* var. *incurvata* represents the greatest elevational gradient of the species, with var. *gigantea* and var. *tenuiretis*, respectively occupying the lowermost and median elevations.

Distribution: *Lescuraea incurvata* var. *incurvata* is very common in North America and has been collected from northern and southern British Columbia, including Vancouver Island; the Selkirk and Omineca Mtn. Ranges of eastern British Columbia; the Rocky Mountains of both British Columbia and Alberta; Waterton Lakes National Park, Alberta; Washington; Montana; Colorado; Utah; California; Oregon; Nevada; Wyoming; and Idaho. It is disjunct in eastern North America in the Keewenaw Peninsula, Michigan, New Hampshire, and in Labrador. This variety has also been collected from several districts in Greenland. *Lescuraea incurvata* var. *incurvata* is equally common in Europe, Scandinavia (including Iceland), the Near East, and parts of Asia.

Specimens examined: ASIA: CHINA: Xinjiang: Tian Shan Mountains: Urumqi Co. – *He 951020* (MO). **Sichuan**: Xiang Cheng Co., Mt. Wu Ming – *He 31799* (MO). **INDIA: Kashmir:** Thajiwas Glacier, near Sonamarg – *Townsend 87/273* (COLO). **NEPAL:** Annapurna Range: Bakreharka below Lamjung Himal *Kunisawa et al.* NICH no.*350698* (MO). **RUSSIA: Bashkiria:** Ural Mountains: South Ural, Beloretzk (COLO). **EUROPE:** *Sommerfeldt 28* (UC/JEPS), *unknown collector 300* (UC/JEPS). Reoult (Jura) – *Müller* (UC/JEPS). **GREECE:** Pindus Mountains (COLO). **ICELAND:** S. of Dalvik, W. side of Akureyri Fjord – *Steere* (US). **NORWAY:** Dovre: Fogshuen – *Bergren* (FH). Montis Flöjfjellet – *Zetterstadt* (FH). **RUSSIA:** Kola Peninsula: Chibiny Mountains, Yukspor Mountain – (COLO). **SCOTLAND:** Perth: Ben Lawyers (COLO). **SPAIN: Santander:** Cordillera Cantabrica, montis Peña Vieja – *Buch* (US). **SUDETEN:** Pfarrkuppe – *Ludwig* anno 1801 (G – lectotype of Leskea incurvata, G – syntypes (6 specimens)). **SWITZERLAND:** Alps: *Bridel* anno 1796 (B – lectotype of Hypnum implexum). **POLAND:** Western Carpathians: Western Tatra Mtns: Tomanowa Valley – *Ochyra 59* (UC/JEPS); Tatry Zachodnie Range – *Wójcicki* (OSC). **RUSSIA:** Murmansk Region: Khibiny Mtns: Yukspor Mtn – *Schljakov* (ALA). **NORTH AMERICA: CANADA: Alberta:** Banff National Park: Lake Louise Area: Lake Agnes – *Krieger & Hebben 1886, 1890, 1984* (ALTA). Jasper National Park: Wilcox Pass – *Lawton 1389b* (WTU), Mt. Wilcox – *Welch 15299* (NY). Waterton Lakes National Park: Cameron Lake – *Krieger & Hebben 1791, 1797, 1804, 1807, 1810* (ALTA), Carthew Lakes –*Ireland 9560A* (CANM), Crandell Lake –*Krieger & Hebben 1820, 1822, 1824, 1827, 1832, 1833* (ALTA), Lower Bertha Falls – *Cook 3024* (CANM), Peak o. Smiles summit – *Bird & Lakusta 16724* (COLO), Rowe Creek – *Krieger & Hebben 1813, 1816* (ALTA). Wilmore Wilderness Area: Hardscrabble Pass – *Krieger 1781, 1789* (ALTA). **British Columbia:** along Green River: at Bella Coola Road – *Norris 2235B* (UC/JEPS). B.C./US border: near Nelway Custom – *Tan & Teng 78-200a* (UBC). Cassiar District: Omineca Mtns – *Ireland & Bellolio-Trucco 18431* (FH). Queen Charlotte Islands: Moresby Island – *Schofield 25056* (UBC). Selkirk Mtns: near Revelstoke: Illicillewaet Canyon – *Macoun 510* (Syntypes of Pseudoleskea falcicuspis – COLO, FH (3 specimens), MICH (2 specimens), UC/JEPS, US (2 specimens)), Roger's Pass – *Macoun 665* (FH), Glacier National Park: Loop Creek Campground – *Krieger & Hebben 1872, 1873, 1876* (ALTA). Vancouver Island: Nanaimo – *Macoun* anno June 8, 1887 (S – Holotype of Pseudoleskea oligoclada, S – isotypes (2 specimens)), *Macoun 670* (US), Strathcona Provincial Park: E. side of Buttle Lake – *Krieger & Hebben 1855* (ALTA). **Northwest Territory:** Logan Mtns: Lake near S. Nahani River – *Vitt 23242* (ALTA). **GREENLAND:** Godthåb district: Praestefjord – *Lewinsky 73-463* (ALA). Narssaq: on Narssaqsund – *Steere 62-957* (US). Sukkertoppen Koloni *Holmen 17.100* (US). **USA: Alaska:** St. Matthew Island: near Glory of Russia Cape – *Schofield 108719* (NY), *108647* (MO). **California:** Siskiyou Co.: S of Big Flat – *Norris 9221* (COLO). Trinity Co.: b/w Ripstein and McKay Camp – *Norris 8024* (UC/JEPS). **Colorado:** Grand Co.: Rocky Mountain National Park – *Rolston 83140* (COLO). Routt Co.: Routt National Forest: Gilpin Lake – *Rolston 84127* (COLO). Boulder Co.: slope of Baldy Peak – *Weber & LaFarge* (COLO). **Idaho:** Blaine Co.: Sawtooth Primitive Area: near Alice Lake – *Hermann 19949* (US).

Bonner Co.: Kanisku National Forest: Reeder Bay Recreation Area – *Hermann 22492* (FH, WTU). **Michigan:** Keeweenaw Co.: Delaware – *Steere* (FH – 2 specimens). **Montana:** Glacier National Park: Logan Pass Area – *Schofield 12107* (OSC), W. bank of McDonald Creek – *Hermann 18270* (WTU). Lake Co.: Mission Mts – *McCune 4247* (COLO). **Nevada:** Elko Co.: Humboldt National Forest: Ruby Mts – *Lawton 2634* (WTU). **New Hampshire:** White Mts: Tuckermann's ravine – *Allen 399* (COLO, MO). **Oregon:** Clackamas Co.: Molalla: Cougar Lake – *Becking 5308055* (UC/JEPS). Linn Co.: Willamette National Forest: Iron Mtn – *Norris 78512* (UC/JEPS). **Utah:** Salt Lake Co.: Big Cottonwood Canyon – *Flowers 1633* (WTU). **Washington:** Chelan Co.: NW of Leavenworth – *Young 50* (WTU). Jefferson Co.: Olympic National Park: to Lake Constance – *Ireland 6469* (FH), *Ireland 6618* (US); Mt. Olympus, Hoh River – *Becking 5309995* (WTU). Pierce Co.: Snoqualmie Forest: White River Ranger District: Mt. Baker – *Buck 30362* (NY). Cascade Mtns: Steven's Pass region – *Grant* (FH). **Wyoming:** Carbon Co.: Battle Creek Canyon: W. slope of Sierra Madre – *Porier & Porier 9715* (COLO). Sublette Co.: Jim Bridger Wilderness Area: Wind River Mts: Shannon Pass – *Rolston 85110* (COLO). Teton National Park: E. of Teton Pass – *Lawton 1783* (WTU).

***Lescuraea incurvata* var. *gigantea* E. Lawton,** Figure 2.27-2.29

Bull. Torr. Bot. Lab. 84(4): 294. 1957.

Type: "Washington, Lawton 2563 (LAWTON)." [Washington, Clallam Co., Olympic Peninsula, Elwha River Valley Trail from Olympic Hot Springs to Boulder Lake, Lawton 2563] **Lectotype – WTU !** (lectotypus); **isotypes – WTU !** (4 specimens); **OSC !, US !, MO !**

Pseudoleskea incurvata var. gigantea (E. Lawton) Crum, Steere, & Anderson, Bryologist 67: 163. 1964.

Nomenclatural notes: *Lescuraea incurvata* var. *gigantea* was described by Lawton (1957), from specimens collected in Washington. In the type citation Lawton (1957) indicated one collection (*Lawton 2563*) as the type. However, according to Dr. R.G. Olmstead (Curator), three packets at WTU were originally designated by Lawton as isotypes and then changed by her to holotype. According to Article 37.1 of the

International Code of Botanical Nomenclature (2000), "publication on or after 1 January 1958 of the name of a new taxon of the rank of genus or below is valid only when the type of the name is indicated." In Article 37.2, "For the name of a new species or infrageneric taxon, indication of the type as required by Art. 37.1 can be achieved by reference to an entire gathering, or part thereof, even if it consists of two or more specimens as defined in Art. 8." Since Lawton (1957) described *L. incurvata* var. *gigantea* before 1 January 1958, a lectotype can be chosen from among the type material. Of these three 'holotype' specimens, one packet is of a thicker paper with a distinct label affixed to the surface. This specimen is chosen as the lectotype. The information on this packet matches the type citation, with the exception of a slight typo on the collection date, which was later corrected. This packet has the typed word 'isotype' on the label, with 'Holo' written overtop in red ink. The other two packets are of a thinner bond paper, with the information typed onto the surface. Similarly, the word 'holo' is written on these packets, but this time above the typewritten word 'isotype'. These two specimens are chosen as isotypes. It is fairly clear that all three specimens are of the same collection as they all contain similar fir needles. However, the packet with the affixed label appears to have belonged in Lawton's personal herbarium before it was incorporated into WTU, and it is for this reason it is chosen as the lectotype.

In addition to the lectotype and isotypes, two other packets at WTU resemble the isotypes mentioned above, with the information printed onto the packet itself. One packet has the hand-written word 'isotype', while the other has no such designation. These are also chosen as isotypes.

Specimens at OSC, MO, and US are all identical to the isotypes at WTU, with the information printed onto the packet. These are also designated as isotypes.

Description: Plants large-sized, distinctly falcate-secund and robust, forming very loosely intertwining mats; yellow-green to green-brown, older stems and branches distinctly orange-brown; dull. Stem apices distinctly hooked; not at all fragile when dry; outer cortical cells of 3 (4) layers. Branching: branches few, 2° branches very few, prostrate. Rhizoids branching slightly; matted tufts common near stem apex. Stem leaves densely arranged; somewhat erect and appressed when dry, the long acumen distinctly flexuose and falcate-secund; somewhat incurved below; slightly biplicate; narrowly long decurrent; ovate-lanceolate, gradually acuminate to a long apex, the acumen distinctly longer or somewhat shorter than the leaf proper; 1.53-2.50 mm long x 0.40-0.90 mm wide, mostly 1.70-2.00 mm long x 0.53-0.80 mm wide. Margins of acumen serrate to somewhat entire; narrowly recurved from lower acumen to leaf base, often with plain sections, sometimes more recurved on one side. Costa somewhat to distinctly percurrent; stout below, narrowing somewhat in acumen; somewhat prorate along upper abaxial portion. Laminal cells slightly echlorophyllose, somewhat opaque to somewhat translucent. Alar cells 4.8-16.8 µm long x 7.2-12.0 µm wide, mostly 7.2-9.6 µm long x 9.6-12.0 µm wide (rarely from 14.4-16.8 µm long). Basal cells quadrate to oblong-rectangular; 7.2-36.0 µm long x 7.2-12.0 µm wide, mostly 14.4-24.0µm long x 7.2 µm wide (rarely from 26.4-36.0 µm long). Median cells elliptic, elliptic-fusiform, to elongate; 4.8-36.0 µm long x 3.6-7.2 µm wide, mostly 12.0-19.2 µm long x 3.6-4.8 µm wide (rarely from 24.0-31.2 µm long). Distal cells 4.8-28.8 µm long x 4.8-7.2 µm wide, mostly 9.6-19.2 µm long x 4.8-7.2 µm wide (rarely greater than 19.2 µm long). Papillae round; prorate; median and distal cells of stem and branch leaves somewhat prorate, sometimes prorae lacking. Perichaetia occasional. Sporophyte rare; few seen. Seta orange to red; 10.0-15.0 mm long. Capsule 1.8-2.5 mm long. Exostome teeth 350-470 µm long. Endostome segments 150-300 µm long. Spores 12.0-21.6 µm in diameter (mostly 14.4-19.2 µm in diameter). N = not reported.

Diagnostic characters: *Lescuraea incurvata* var. *gigantea* is distinguished by: 1) distinctly falcate-secund and extremely robust plant habit; 2) very few branches; 3) ovate-lanceolate and gradually acuminate leaves; 4) leaves somewhat incurved below, with the long acumen flexuose and distinctly falcate-secund; 4) an acumen distinctly longer or rarely as long as the leaf proper; 5) not or indistinctly prorate distal and median cells, the lumens not leading into the prorae; and 6) predominantly terricolous over siliceous or alkaline rocks, boulders, and outcrops, often among other bryophytes. *Lescuraea incurvata* var. *gigantea* is the large form of the species, with var. *tenuiretis* and var. *incurvata*, respectively small and intermediate. Although the range in leaf and laminal cell sizes of *L. incurvata* var. *gigantea* overlaps with the upper leaf and laminal cell sizes of var. *incurvata*, leaf shape including the attributes of the acumen, papillosity, habitat and substrate are limited mostly to this variety.

Variation: Most of the variation in *Lescuraea incurvata* var. *gigantea* is in leaf length and width, 1.53-2.50 mm long x 0.40-0.90 mm wide (usually 1.70-2.00 mm long x 0.53-0.80 mm wide), with the shape and size of the laminal cells variable, yet predominantly elliptic and rounded.

Habitat: *Lescuraea incurvata* var. *gigantea* occurs predominantly on mesic soil and humus over siliceous and alkaline boulders, rock outcrops, and cliff faces in mixed conifer (*Tsuga heterophylla* and *Pseudotsuga menziesii*) and deciduous forests (*Quercus* sp., *Acer* sp.) of the west coast, often among other bryophytes. This variety also occurs in *Larix* sp. and *Pinus monticola* communities, often with patches of *Thuja* sp. and *P. menziesii*, along its interior (SE British Columbia-Idaho) range. *Lescuraea incurvata* var. *gigantea* is occasionally found near streams and other water sources. Elevation: approximately 610-2135 metres (mostly 1000-1400 m, rarely less than 900 or greater than 1700 m). *Lescuraea incurvata* var. *gigantea* occupies the lowermost elevations of the species complex.

Distribution: *Lescuraea incurvata* var. *gigantea* has been collected from southwestern British Columbia, including Vancouver Island, as well as from northwestern portions of Washington, Oregon, and California. One collection has been made along the coast of central British Columbia. This variety is uncommon east of the Cascade Mountains. However, a smaller range appears to extend from southeastern British Columbia into north and central Idaho. It is suspected that *Lescuraea incurvata* var. *gigantea* could occur along the entire coast of British Columbia, presumably into mainland Alaska as well. There is no evidence that this variety exists in Europe.

Specimens examined: NORTH AMERICA: CANADA: British Columbia: Champion Lakes Provincial Park: Three Lakes – *Tan & Ensing 77-160* (UBC). Garibaldi: near Green River – *Schofield & Lang 26202* (CANM). Kleanza Creek Area: Skeena River – *Schofield & Boas 21084* (UBC). Seymour Arm: Shuswap Lake – *Brinkman 611* (MO).

near Slocan Creek Park Municipality: Airy Creek – *Tan & Ensing 77-560* (UBC). Vancouver Island: Nanaimo: Mt. Benson – *Macoun 570* (COLO); Strathcona Provincial Park: E. side of Buttle Lake – *Krieger & Hebben 1865, 1866, 1867, 1869* (ALTA). Ymir Municipality: Ymir Creek – *Tan & Ensing 77-1306* (UBC). **USA: California:** Humboldt Co.: E. of Hoopa: S. Fork of Tish Tang a Tang Creek – *Norris 52412* (UC/JEPS). Tehama Co.: E. of Mineral: Battle Creek – *Norris 48163* (UC/JEPS). **Idaho:** Bonner Co.: E. side of Priest Lake: Indian Creek – *Ireland 8642* (COLO). Idaho Co.: Clearwater National Forest: Lochsa lodge – *Hermann 20214* (MICH). Latah Co.: Moscow Mtn – *Alex & Higinbotham* (CANM). Traille River basin: S. end of Lake Pend'Oreille – *Leiberg 141* (CANM). **Oregon:** Multnomah Co.: Larch Mtn: near Sherrard Point – *Schofield 19748* (UBC). **Washington:** Clallam Co.: Olympic National Park: between Olympic Hot Springs and Boulder Lake – *Lawton 2563* (WTU – lectotype of Pseudoleskea incurvata var. gigantea, isotypes –WTU (4 specimens), MO, OSC, US), *Lawton 4167* (WTU). Easton: Kitchelos Lake – *Röll 687, 830, 853* (FH). Glacier Peak Wilderness Area: near Portal Peak Summit – *Benkinson 240* (UC/JEPS). Jefferson Co.: Olympic National Park: Lake Constance – *Ireland 6618* (US). Mt. Rainier National Park: W. of St. Andrew's Creek – *Lawton 5086* (UC/JEPS).

***Lescuraea incurvata* var. *tenuiretis* (Culm.) E. Lawton,** Figure 2.30-2.32
Bull. Torr. Bot. Cl. 84: 294. 26-27. 1957.

Pseudoleskea filamentosa var. *tenuiretis* Culm., Rev. Bryol. 37(5): 94. 1910.

Type: "Dans une dépression humide entre le col de la Grimsel et le Siedelhorn à 2300 m. avec le P. patens sur terrain siliceux (gneiss). -- Cette variété sera distribuée dans la Bryotheca Europaea de M. Bauer." [legit Culmann] **Lectotype – Z !** (lectotypus); **isotypes – Z !, FH !** (Bauer, exs. 1225)

Pseudoleskea atrovirens var. *tenuiretis* (Culm.) Giac., Annali Bot. 23: 7. 1946.

Pseudoleskea incurvata var. *tenuiretis* (Culm.) Podp., Consp. 531. 1954.

Nomenclatural notes: *Pseudoleskea filamentosa* var. *tenuiretis* was described by Culmann in 1910 from specimens collected in Switzerland on September 8, 1908. Type material from Z consists of two packets, both with nearly identical information. The label on the packet identified in Z as $(^{41/99T}/_{1})$ indicates that the specimen is a mixed collection of *Pseudoleskea filamentosa* var. *tenuiretis* and *P. patens*. The remainder of the information also corresponds with the type citation. The label on the second packet identified in Z as $(^{41/99T}/_{2})$ is nearly identical to the first. However, it does not indicate that the specimen is a mixed collection. After having examined both sterile specimens, it is clear that they are from the same collection, both containing *P. patens*. Since the packet label in Z as $(^{41/99T}/_{1})$ indicates the mixed collection of *Pseudoleskea filamentosa* var. *tenuiretis* and *P. patens* (= *Lescuraea patens*), this specimen is chosen as the lectotype. The second packet in Z as $(^{41/99T}/_{2})$ is chosen as an isotype.

In the type citation, Culmann (1910) also indicated that exsiccates of *Pseudoleskea filamentosa* var. *tenuiretis* were distributed by Bauer. A single specimen at FH with 'Bauer, Musci eur. exs. 1225' corresponds exactly with both the type citation and the packet labels in Z, and is therefore designated as an isotype.

Lawton (1957) indicated that the holotype of *P. filamentosa* var. *tenuiretis* is at LAU. However, Culmann's collection is actually housed at Z. It is evident that Lawton did not review the type material at Z, as no annotation slips were provided. Since Culmann's collection is at Z, I feel confident in chosing a lectotype from this herbarium, and not from LAU. The specimen from LAU has not been examined.

Description: Plants small-sized, julaceous and robust, forming densely intertwining mats; green with orange tinges to green-brown, older stems and branches distinctly orange-brown to brown-black; dull. Stem apices somewhat hooked; slightly fragile when dry; outer cortical cells of 3 (2) layers. Branching: branches numerous, 2° branches numerous, often erect. Rhizoids branching slightly; matted tufts uncommon near stem apex. Stem leaves densely arranged; julaceous and appressed when dry, the short acumen distinctly incurved; distinctly concave throughout; not falcate-secund; distinctly biplicate; narrowly short decurrent; ovate, abruptly acuminate to a short apex, the acumen distinctly shorter than the leaf proper; 0.75-1.20 mm long x 0.34-0.78 mm wide, mostly 0.84-1.10 mm long x 0.43-0.66 mm wide. Margins of apex distinctly serrate to crenate, acumen distinctly serrate to crenate; broadly to somewhat narrowly recurved from middle acumen to leaf base, sometimes more so on one side. Costa ending abruptly in mid acumen, rarely to upper acumen; stout throughout; distinctly prorate along upper abaxial portion. Laminal cells chlorophyllose, opaque. Alar cells 4.8-16.8 µm long x 7.2-9.6 µm wide, mostly 7.2-9.6 µm long x 9.6 µm wide (rarely from 14.4-16.8 µm long). Basal cells quadrate to short-rectangular; 4.8-31.2 µm long x 7.2-9.6 µm wide, mostly 9.6-19.2 µm long x 9.6 µm wide (rarely from 26.4-31.2 µm long). Median cells isodiametric and angular to somewhat short-rhomboidal; 4.8-21.6 µm long x 7.2-12.0 µm wide, mostly 7.2-14.4 µm long x 7.2 µm wide (rarely from 16.8-21.6 µm long). Distal cells 4.8-19.2 µm long x 7.2-9.6 µm wide, mostly 7.2-12.0 µm long x 7.2 µm wide (rarely from 16.8-19.2 µm long). Papillae angular; prorate; median and distal cells of stem and branch leaves distinctly prorate. Perichaetia occasional. Perigonia not seen. Sporophyte rare; very few seen. Seta orange to red; 7.0-8.5 mm long. Capsule 1.0-2.0 mm long. Exostome teeth 317-375 µm long. Endostome segments 223-225 µm long. Spores 12.0-19.2 µm in diameter (mostly 12.0-16.8 µm in diameter). N = not reported.

Diagnostic characters: *Lescuraea incurvata* var. *tenuiretis* is distinguished by: 1) a julacous and 'compact' plant habit; 2) numerous branches; 3) ovate and abruptly acuminate leaves; 4) leaves distinctly incurved, with the acumen also incurved; 4) an acumen distinctly shorter than the leaf proper; 5) angular and distinctly prorate distal and median cells, lumina of which can be seen to obliquely extend into the prorae; and 6) predominantly saxicolous on alkaline rocks, boulders, and outcrops.

Lescuraea incurvata var. *tenuiretis* is the compact form of the species, with var. *incurvata* and var. *gigantea*, respectively intermediate and large. Although the range in leaf and laminal cell sizes of *L. incurvata* var. *tenuiretis* overlaps with the lower leaf and laminal cell sizes of var. *incurvata*, leaf shape, including the attributes of the acumen, are limited mostly to this variety.

Variation: Most of the variation in *Lescuraea incurvata* var. *tenuiretis* is in leaf length and width, 0.75-1.20 mm long x 0.34-0.78 mm wide (usually 0.84-1.10 mm long x 0.43-0.66 mm wide), with the shape and size of the laminal cells variable, yet predominantly isodiametric and angular.

Habitat: *Lescuraea incurvata* var. *tenuiretis* occurs on dry alkaline boulders and outcrops in forests and in intermittent streambeds, as well as forming dense mats on alkaline and sometimes siliceous outcrops in subalpine meadows. It is sometimes found on soil and on mesic siliceous boulders. Elevation: approximately 1465-2380 metres (mostly 1700-2200 m). *Lescuraea incurvata* var. *tenuiretis* seems to be intermediate between *L. incurvata* var. *incurvata* and *L. incurvata* var. *gigantea* in its elevational gradient.

Distribution: *Lescuraea incurvata* var. *tenuiretis* is not very common in North America, although it has been collected from Vancouver Island, British Columbia; Banff, Waterton Lakes National Park, and Oldman River watershed in Alberta; Montana; and California. A few specimens have been collected from Utah. This variety has also been collected from Slovakia and from the Alps in Europe.

Specimens examined: EUROPE: ALPS: Karwendelgebirge: Mittenwald – *Hübschmann* (UBC). **SLOVAKIA**: Tatra Mountains: Monte Suchý – *Pilous 169* (UBC). **SWITZERLAND:** Grimselpasshöhe und Siedelhorn – *Culmann* anno 8.9.1908 (Z – lectotype of Pseudoleskea filamentosa var. tenuiretis, Z – syntypes (6 specimens)). **NORTH AMERICA: CANADA: Alberta:** Banff National Park: Lake Louise – *Crum & Schofield 3813* (UBC). NNW of Coleman: Racehorse Pass – *Bird & Lakusta 18117* (COLO). Waterton Lakes National Park: SW of Pincher Creek– *Bird & Lakusta 14972* (CANM, COLO), Forum Peak – *Crum & Schofield 5766* (CANM), *Doubt 2534* (ALTA), N. side of Crandell Lake – *Krieger & Hebben 1824, 1826, 1827, 1830* (ALTA), Blakiston Creek – *Krieger & Hebben 1830* (ALTA). Bow River Watershed: W. of Kananaskis Lake – *Bird & Glenn* (CANM), NW of Lower Kananaskis Lake – Bird *& Glenn 12962* (CANM). Wilmore Wilderness Area: Middle Persimmon Range: Jacknife Pass – *Krieger 1778* (ALTA). **British Columbia:** Vancouver Island: Strathcona Provincial Park: Marble Meadows – *Halbert 7861* (UBC), *Spence & Glass 1376* (UBC). **USA: California:** El Dorado Co.: near Twin Bridges Campground – *Norris 58505* (UC/JEPS). Siskiyou Co.: Marble Mtn Wilderness Area: Little Marble Valley – *Spjut 1126* (UC/JEPS). **Montana:** Flathead Co.: near Swan Range Crest – *McCune 4720* (OSC). Glacier Co.: Hanging Gardens: Logan Pass – *Hermann*

18071 (CANM). **Utah:** Cache Co.: N. of Tony Grove Lake – *Behling 246* (FH). Salt Lake Co.: Wasatch Mtns: Big Cottonwood Canyon – *Flowers 1642* (COLO).

Lescuraea patens (Lindb.) Arn. & C. Jens., Figures 2.33-2.35

Naturw. Unt. Sarekgeb. Schwed.-Lapp. 3: 212. 1910.

Lesquereuxia patens Lindb., Medd. Soc. Fauna Fl. Fenn. 14: 75. 1888.

Type: "*Hab.* Norvegia, Hardanger, in alpe inter Graven et Ulvik (♀ ster., Aug. 31, 1874, N. Wulfsberg). Suecia, prov. Vestergöthland, in pariete perpediculari rupis diabas. Ad latus septemtrionale cacuminis in monte Ålleberg (♂, Junii 28, 1880, S.O.L.)." **Lectotype – H-SOL !** (*Wulfsberg*, lectotypus); **syntype** – (*Lindberg*, not available from **H-SOL**)

Pseudoleskea ticinensis Bott., Atti della Soc. Tosc. de Sci. Nat. di Pisa, Memorie 7: 202. 1891. *Fide* Wijk *et al.* 1967; Redfearn 1986.

Type: protologue unavailable

Pseudoleskea atrovirens var. *patens* (Lindb.) Conr. & Hag., Forh. Vid. Selsk. Christiana 1893 (11): 20. 1893.

Pseudoleskea patens (Lindb.) Kindb., Canad. Rec. Sc. 6: 20. 1894. *Fide* Ignatov & Afonina, 1992.

Pseudoleskea heterocladioides Kindb., Rev. Bryol. 22: 83. 1895.

Type: "*Eur.* Norway: J. Hagen. (Pseudoleskea patens *Limpricht Laubm*)." **Holotype – S !**

Pseudoleskea patens subsp. *heterocladioides* (Kindb.) Kindb., Skand. Bladm. 26. 1903.

Pseudoleskea atrovirens var. *ticinensis* (Bott.) Bott., Atti della Soc. Tosc. de Sci. Nat. di Pisa, Memorie 29: 159. 1913.

Lescuraea atrovirens var. *patens* (Kindb.) Moenk., Laubm. Eur. 692. 1927.

Pseudoleskea filamentosa subsp. *patens* (Lindb.) Culm. & Amann, Flore des Mousses de la Suisse 2: 283. 1918.

Pseudoleskea atrovirens subsp. *patens* (Lindb.) Giacom., Atti de Ist. Bot. "Giovanni Briosi" e Lab. Critt. Ital. No del. R. Univ. di Pav. Ser. 5. 4: 256. 1947.

Nomenclatural notes: In 1881, Lindberg listed his new species *Leskea patens*, in a publication by Saelan. Unfortunately, he failed to provide a description. As such, this name was invalid. In 1888, Lindberg finally described and published his new species as *Lesquereuxia patens*, using *Lesquereuxia* as his alternative spelling of *Lescuraea*. Of the two syntypes listed above, one was collected in 1874 by Wulfsberg and the other in 1880 by Lindberg himself. Only the former specimen was received from H-SOL, and it matches the type information given. According to Lawton (1957), Lindberg's specimen is the holotype of *Lesquereuxia patens*, and is at S-PA. The location of Lindberg's specimen at S-PA has not been verified. As Lindberg initially revealed his new species in 1881, the Wulfsberg specimen has the handwritten name *Leskea patens*. The Wulfsberg specimen is chosen here as the lectotype.

The protologue for *Pseudoleskea ticinensis* Bott. has not been obtained, thus type material has not been reviewed. Wijk *et al.* (1967) and Redfearn (1986) consider *P. ticinensis* synonymous with *P. patens*.

Pseudoleskea heterocladioides was described by Kindberg in 1895 for a specimen collected by Hagen in Norway. The holotype is at S, and the packet label indicates that Hagen collected the specimen in Trondheim on April 20, 1894. Wijk *et al.* (1967) also consider *Pseudoleskea heterocladioides* a synonym of *L. patens*.

Description: Plants very small to small, rarely medium-sized; julaceous, forming densely intertwining mats; green to dark green, with older stems and branches brown; distinctly dull. Stems prostrate, thin; apices somewhat to distinctly hooked; somewhat to distinctly round when dry or moist; fragile when dry; outer cortical cells of 2-3 layers, orange to orange-red, thick-walled; cells of medulla thin-walled, rounded, gradually large-lumened, hyaline; central strand present . Branching irregularly, branches numerous, 2° branches numerous; usually short and prostrate. Rhizoids smooth; red-brown; occasional; branching slightly; forming tufts along stems; matted tufts common near stem apex; few along branches. Paraphyllia multiform, filamentous to foliose, unbranched; cells thick-walled, rhomboidal to elongate; numerous on younger portions of stems and branches. Stem leaves densely arranged; julaceous to tumid when dry, spreading or patent when moist, the short acumen incurved; distinctly concave throughout; asymmetric to slightly symmetric; indistinctly plicate or plicae lacking; broad and somewhat short decurrent; ovate and abruptly acute to rarely ovate-lanceolate and slightly acuminate, acumen distinctly shorter than the leaf proper; 0.68-0.98 mm long x 0.29-0.64 mm wide, mostly 0.72-0.83 mm long x 0.33-0.52 mm wide. Branch leaves similar in shape to stem leaves, somewhat smaller, more distinctly serrate at apex. Margins distinctly serrate to dentate at apex, acumen somewhat dentate; narrowly recurved from lower acumen to leaf base. Costa ± orange-tinged, mostly green; ending well before apex; very stout below, remaining stout above; abaxial surface distinctly keeled; highly prorate along upper abaxial portion. Laminal cells distinctly chlorophyllose and opaque. Alar region large, extending more than ⅓ up leaf margin; cells thick-walled, not at all lax; quadrate to transversely elongate; 7.2-14.4 μm long x 9.6-14.4 μm wide, mostly 7.2-9.6 μm long x 9.6-12.0 μm wide (rarely from 12.5-15.0 μm long). Basal cells thick-walled, not at all lax or pitted; quadrate to somewhat rectangular, with few irregular or elongate cells interspersed; 7.2-16.8 μm long x 7.2-12.0 μm wide, mostly 9.6-12.0 μm long x 9.6-12.0 μm wide (rarely from 14.4-16.8 μm long or less than 9.6 μm long). Median cells thick-walled; mostly homogeneous from costa to mid-leaf; isodiametric to quadrate, occasionally slightly rhomboidal or fusiform-rhomboidal cells interspersed, cells of margin quadrate to somewhat elongate; 7.2-16.8 μm long x 4.8-12.0 μm wide, mostly 7.2-12.5 μm long x 7.2-9.6 μm wide (rarely from 14.4-16.8 μm long or less than 7.2 μm long). Distal cells thick-walled; isodiametric, usually becoming somewhat rhomboidal near apex; 7.2-16.8 μm long x 4.8-9.6 μm wide, mostly 7.2-9.6 μm long x 7.2-9.6 μm wide in the lower portion, 12.0-16.8 μm long x 9.6 μm wide in upper portion. Papillae round to somewhat long and narrow; on central cell lumen, sometimes on upper cell lumen of some rhomboidal to elongate cells; median and distal cells distinctly papillose, reaching most lower cells; stem and branch leaves equally papillose; papillae common on abaxial and adaxial leaf surfaces. Perichaetia common, satin and translucent; perichaetial leaves erect, lanceolate, abruptly short acuminate, somewhat serrate above; clasping seta throughout; costa somewhat stout below, narrower above, extending into upper acumen; basal cells lax, oblong-rectangular, distal and median cells somewhat thick-walled, fusiform; papillae lacking. Perigonia occasional, limited to several along stems or branches; perigonial bracts ovate, abruptly acuminate, appressed, concave and entire;

ecostate; basal cells lax, oblong-fusiform, distal and median cells thick-walled, fusiform-linear; papillae lacking. Sporophyte occasional to common. Seta smooth; orange to red-brown; dextrorse below, somewhat to distinctly sinistrorse above; 7.0-14.5 mm long (rarely greater than 1.20 mm). Capsule distinctly arcuate, cylindric, and asymmetric; orange to red-brown; somewhat rough and dull; distinctly constricted below mouth when dry, mouth flaring outward, swollen when moist; 0.5-2.0 mm long, mostly 0.1 mm long. Operculum short-rostrate. Peristome inserted along mouth of capsule. Exostome teeth orange-brown below, yellow-hyaline above; lanceolate, ± abruptly acuminate, distinctly 'shouldered'; incurved, distal portion vanishing between endostome segments; joined at base to form an orange-red to red-brown band; proximal dorsal surface with fine horizontal papillose-striae to ½ or ⅔ height of tooth, fine papillose-striae in oblique or circular pattern in median portion, sparse and rounded papillose in distal portion of tooth; apex somewhat sharp; ventral surface distinctly trabeculate; 310-490 µm long, mostly 400-417 µm long. Endostome segments yellowish-hyaline; as long to distinctly longer than exostome; linear-lanceolate, distinctly keeled, straight, not inflexed; narrowly perforate along median line; narrowly spaced, joined to form a high basal membrane of similar colour ⅓ to nearly ½ height of segments; dorsal and ventral surfaces sparse and minutely papillose throughout; 200-270 µm long (rarely less than 200 µm or greater than 300 µm long); cilia filiform, 1-3, to nearly ½ height of segments, sometimes broken off at base, appendiculate, minutely papillose throughout. Spores minutely papillose; 9.6-14.4 µm in diameter, mostly 9.6-12.0 µm in diameter. N = 11 (Fritsch 1982).

Diagnostic characters: *Lescuraea patens* forms small or rarely medium-sized, dark green mats on cliff faces and on boulders. This taxon has julaceous stems and branches, with 2° branches common. Laminal cells are mostly isodiametric and distinctly chlorophyllose. A single round or long and narrow papilla is common over the central cell lumen of most laminal cells. The lanceolate exostome segments are beset with fine horizontal papillose-striae to nearly ⅔ the height of the tooth, and are distinctly shouldered. The basal membrane of the endostome is nearly ½ the height of the segments, and cilia are distinctly filiform and common. Based on the above diagnostic characters, this species is rarely mistaken for any other taxon in *Lescuraea*. The taxon

Lescuraea incurvata is somewhat similar gametophytically with julaceous or incurved leaves, thick-walled cells, and irregular and highly variable laminal cells, including having almost exclusively transversely elongate alar cells. However, laminal cells are distinctly prorate, that is papillae do not cover the central lumen (as in *L. patens*). In addition, the height of the endostomal basal membrane in *L. incurvata* is only to ⅓ the height of the segments.

Gametophytically, *Lescuraea patens* is somewhat similar to *Leskea*. However, taxa in *Leskea* are very small in size. Similarly, where *Lescuraea patens* has numerous paraphyllia, taxa in *Leskea* do not. Sporophytically, they are quite different and cannot be confused with one another. *Lescuraea patens* has an arcuate, cylindric, asymmetric capsule, and lanceolate exostome teeth that are 'shouldered'. The endostome segments in *L. patens* are also distinctly keeled, and the basal membrane is high. Capsules in *Leskea* on the other hand, are erect to slightly inclined, distinctly long cylindric, and symmetric. The exostome teeth are linear-lanceolate and indistinctly 'shouldered'; the endostome segments are terete, and the basal membrane is medium or low.

Variation: Leaf length and width varies from 0.68-0.98 mm long x 0.29-0.64 mm wide (usually 0.72-0.83 mm long x 0.33-0.52 mm wide) both within and between specimens. In some leaves, numerous cells are less isodiametric and more rhomboidal or elongate; resulting in papillae that tend to occur over the upper cell lumen.

Habitat: *Lescuraea patens* occurs on boulders in forests and thickets and on shaded rock outcrops, often near streams or other water sources. It is rarely found on soil, bases of trees, and on litter; but when present then usually near moist areas. Elevation: approximately 970-3250 metres (occasionally less than 300 m).

Distribution: *Lescuraea patens* has been collected from: the Aleutian Islands and Alexander archipelago in Alaska; the Northwest Territory; northern and southern British Columbia, including Queen Charlotte and Vancouver Islands, Selkirk and Purcell Mountain ranges; the Rocky Mountains of both British Columbia and Alberta; Waterton Lakes National Park, Alberta; Washington; the northwestern portions of Montana and Colorado; Utah; California; Oregon; and Wyoming. A single specimen has been seen from Saskatchewan and from Nevada. It is disjunct in eastern North America in the Keewenaw Peninsula, Michigan; Cape Breton, Nova Scotia; Newfoundland; and New Hampshire. This species is also common in Europe, Scandinavia, and several localities in Scotland and in Asia.

Specimens examined: ASIA: KOREA: Tongduch'on-shi Co.: *Shevock 16175* (UC/JEPS). **EUROPE: DENMARK: Faroe Islands:** Østero: Slattaretindur – *Jensen* (US). **NORWAY:** *Hagen* (S – holotype of Pseudoleskea heterocladioides), Hardanger – *Wulfsberg* Aug. 31, 1874 (H-SOL – lectotype of Lesquereuxia patens). **SCOTLAND:** Forfar: Caenlochan Glen – *Perry* (US). Perth: Ben Lawers – *Perry* (US). **NORTH AMERICA: CANADA: Alberta:** Banff National Park: Lake Louise – *Crum & Schofield 3813* (WTU), Lake Agnes – *Krieger & Hebben 1897, 1898, 1899* (ALTA), Parker Ridge – *McCune 4139* (OSC). Kananaskis Country: Highwood Pass – *Krieger 1709* (ALTA). Waterton Lakes National Park: *Hermann 20570 ½* (CANM), Rowe Trail near Akimina highway – *Doubt 4634* (ALTA), Rowe Creek Trail – *Krieger & Hebben 1813, 1814, 1815, 1816, 1817, 1818, 1822, 1828* (ALTA), descent from Summit Lake to Cameron Lake – *Doubt 6410* (ALTA). **British Columbia:** Bugaboo Glacier Provincial Park – *Tan & Teng 78-1084* (UBC). Champion Lake Provincial Park – *Tan & Ensing 77-30* (UBC). Glacier National Park: *Tan 77-1824* (UBC), Loop Creek Campground – *Krieger & Hebben 1875* (ALTA). Hudson Bay Mtn – *Schofield, Vitt & Horton 73130* (CANM). Kokanee Glacier Provincial Park – *Tan & Ensing 77-808* (UBC). North Vancouver: Mount Seymour Provincial Park – *Krieger & Hebben 1834, 1837, 1839, 1843, 1844, 1845, 1847, 1848, 1849, 1850* (ALTA). Queen Charlotte Islands – *Schofield & Spence 84101* (CANM). Sandon District: *MacFadden* (COLO), Jackson Basin – *Grout* (DUKE). Vancouver Island: *Halbert 7944* (CANM), Strathcona Provincial Park: E. side of Buttle Lake – *Krieger & Hebben 1853, 1862, 1863* (ALTA), W. side of Buttle Lake – *Krieger & Hebben 1864* (ALTA). **Newfoundland:** Cape Ray-Burgeo – *Tuomikoski 1903* (CANM). Highlands of St. John: Doctor's Hill – *Tuomikoski 4541* (CANM). **Northwest Territories:** Mackenzie District: Lake close to S. Nahani River – *Schofield, Vitt & Horton 70721* (DUKE). **Nova Scotia:** Victoria Co. – *Belland 92131* (UBC). Cape Breton Highlands National Park – *Belland, Schofield & Weber 10666* (UBC). **USA: Alaska:** Aleutian Islands: Attu Island – *Van Schmack 333*

(MICH), Izembek National Wildlife Reserve – *Schofield & Talbot 99744* (ALA), Kodiak Island – *Sharp 195* (MO), Simeonof Island – *Schofield 106271* (DUKE, NY), Unalaska Island – *Schofield 104547* (UBC). Alexander Archipelago: Chichagof Island – *Wagner 4249* (NY), Chisik Island – *Talbot 87003-7, 87040-13* (NY), Juneau – *Mehner* (CANM), Yakutat – *Stair 5044* (MICH). Mainland: Kodiak Island – *Sharp 195, 211* (NY), S. Haines – *Darigo 2952* (MO). Probilof Islands – *Schofield 108308* (MO). **California:** Amador Co. – *Norris 82737* (UC/JEPS). Del Norte Co. – *Norris 70825* (UC/JEPS). El Dorado Co. – *Whittemore 4182* (MO). Fresno Co. – *Shevock & York 12424* (UC/JEPS). Humboldt Co. – *Norris 70648* (UC/JEPS). Mariposa Co. – *Norris 85348* (UC/JEPS). Siskiyou Co. – *Homberg 952* (F). Trinity Co. – *Norris 56880* (UC/JEPS). Tuolumne Co. – *Wiggins* (DUKE). **Colorado:** Boulder Co. – *Hermann 82137* (COLO). Larimer Co. – *Flowers 4981* (COLO). Mesa Co. – *Hermann 26515a* (WTU). Routt Co. – *Hermann 25718* (COLO). San Juan Co. – *Schofield & Jamieson 82982, 83345* (UBC). **Idaho:** Blaine Co. – *Hermann 20121* (NY). Elmore Co. – *Sharpe 17786* (MO). **Michigan:** Keeweenaw Peninsula – *Sharp 37* (COLO). **Montana:** Glacier Co. – *Hermann 20475* (UBC). Lincoln Co. – *Flowers 6670* (COLO). Missoula Co. – *Harvey & McCune 3121/5111* (OSC). Ravalli Co. – *McCune 4057* (OSC), *4606* (COLO). Sanders Co. – *Anderson 22718* (UBC). **Nevada:** Ormsby Co.: E. of Lake Tahoe – *Lawton 3123* (WTU). **New Hampshire:** Coos Co.: Lake of the Clouds: Mt. Washington – *Faxon 358?* (NY). **Oregon:** Clatsop Co. – *Schofield & Tan 68403* (UBC). Grant Co. – *Schofield & Lyford 73946* (UBC). Jefferson Co. – *Wagner 2334* (OSC). Lane Co. – *Schofield & Lyford 73718* (UBC). Linn Co. – *Allen 834* (MO). Umatilla Co. – *Flowers 3824* (COLO). **Utah:** Duchesne Co. – *Flowers 3200* (UBC). Salt Lake Co.: Lamb's Canyon – *Flowers 2830* (ALA). Sevier Co. – *Flowers 4638* (COLO). **Washington:** Chelan Co. – *Ireland 8088* (MO). King Co. – *Lawton 3556* (MO). Klickitat Co.: along Highway 97 – *Lawton 4662* (WTU). Lewis Co. – *Ireland 8038* (CANM, MO). Olympic National Park – *Harthill 3660* (COLO). Pierce Co. – *Lawton 4832* (UC/JEPS), *Ireland, Lawton & Sharp 9136* (CANM). Snohomish Co. – *Schofield, Ireland & Boas 18561* (UBC). Yakima Co. – *Ireland & Lawton 8405* (CANM). **Wyoming:** Carbon Co. – *Hermann 25598* (F).

Lescuraea radicosa (Mitt.) Mönkem., * Figure 2.36-2.40

Die Eur. Laubm. 2: 414. 60 f.1. 1904.

Leskea brachyclados Schwägr. *in* Schultes, Reise auf den Glockner 2: 364. 1804. ***synon. nov.*** **Type:** "Ad terram et Saxa inter glacies *Salmshöhe*." **Lectotype – G !** (lectotypus)

Pseudoleskea atrovirens var. *brachyclados* (Schwägr. *in* Schultes) Bruch & Schimp. *in* B.S.G., Bryol. Eur. 5: 148. 477 ß. 1852.

Hypnum radicosum Mitt., Jour. Linn. Soc. Bot. 8: 31. 1865.

Type: "*Hab.* Banks of the Portage River, *Drummond*, no. 225 (*H. tenax*)." in part. **Lectotype – NY !** (lectotypus); **isotype – NY !**

Pseudoleskea brachyclados (Schwägr. *in* Schultes) Kindb., Mém. de la Soc. Sci. Nat. Cherbourg 24: 324. 1884.

Lescuraea brachyclados (Schwägr. *in* Schultes) Kindb., Rev. Bryol. 12: 29. 1885.

Pseudoleskea sciuroides Kindb. & Macoun *in* Macoun, Bull. Torr. Bot. Cl. 17: 276. 1890. **Type:** "On rocks in the valley of Elk River, Rocky Mountains, B.C., 1883. Dr. G.M. Dawson coll." [Canada] **Holotype – S !**

Lescuraea filamentosa var. *brachyclados* (Schwägr. *in* Schultes) Broth., Act. Soc. Sc. Fenn. 19(12): 119. 1891.

Ptychodium pfundtneri Limpr., Die Laubm. 2: 796. 1895.

Type: "**Schweiz:** Eggischhorn Wallis 2400 m. cfrct. (J.Weber 27. Juli 1887); **Voralberg:** Geweihkopf bei Schruns 2400 m. cfrct. (Breidler 18. Juli); **Tirol:** Rothmoosthal bei Obergurgl 2300 m., steril ♀ (Breidler 12. September 1872); Möserlingwand 2300 m, ♂ Exemplare (Breidler 12. August 1872); **Salzburg:** Ober-Salzbachthal 2800 m, Lissachthal 2300 m und Kareck bei St. Michael, Lungau 2400 m, ♀ Exemplare, Kranzspitz 2000 m, Liegnitzkar 1600-1800 m und Steinriesthal bei Schladming 1400-1600 m, Knallstein in der Sölker Alpen 2000 m, Seekarspitz am Radstadter Tauern, Winterleiten bei Judenburg 1800 m, Eisenhut bei Turrach 1900-2000 m und Hochalpe bei Turrach 2000 m (sämtlich von

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*** Proposal to conserve name to be validated separately**

J.Breidler); **Kärnten:** Lanischkar in Katschthale 2500 m (*Breidler* 29. August 1878)." **Lectotype – BP !** (*Weber*, lectotypus); **syntypes – BP** (none seen)

Pseudoleskea pfundtneri (Limpr.) Kindb., Eur. and N.Am. Bryin. (Mosses) 1: 53. 1897.

Pseudoleskea bicolor Kindb., Eur. and N.Am. Bryin. (Mosses) 1: 53. 1897.

Type: "Schistose alp. rocks r. *Eur.* Sweden in Lapland near Lake Virijaur: E. Nyman 1893." **Holotype – S !; isotype – S !**

Pseudoleskea denudata var. *holzingeri* Best, Bull. Torr. Bot. Cl. 27(5): 229. 1900.

Type: "On the ground at high altitudes; collected by J.M. Holzinger and J.B. Blake near Lake McDonald, northwestern Mont., July 28, 1898, and by R.S. Williams in fruit near Columbia Falls, Mont., Oct. 10, 1895. A smaller form of what appears to be the same by Dr. Bell at Cape Chudleigh, Hudsons Strait; in Professor Macoun's collection. Bryoth. Mont. no. 343, R.S. Williams." **Lectotype – NY !** (*Williams*, lectotypus); **isotype – F !** (*Williams*, 2 specimens); **syntype – NY !** (*Holzinger* and *Blake*); **isotype – FH !** (*Holzinger and Blake*)

Pseudoleskea jemtlandica Kindb., Skand. Bladmfl. 27. 1903.

Type: "Fjellklipp. r.r. *Sver*. Jtl. Stenfjellet vid Storlien: E. Adlerz 1882." **Holotype – S !; isotype – S !**

Ptychodium bicolor (Kindb.) Roth., Die Eur. Laubm. 2: 414. 60 f.1. 1904.

Pseudoleskea radicosa var. *holzingeri* (Best) Hag., K. Norsk. Vid. Selsk. Skrift. 1908(9): 65. 1909.

Pseudoleskea atrovirens var. *pfundtneri* (Limpr.) Bott., Atti. Soc. De Sci. Nat. di Pisa, Mem. 29: 155. 1913.

Pseudoleskea incurvata var. *brachyclados* (Schwägr. *in* Schultes) Card. *in* Tourret, Bull. Soc. Bot. France 60: CCXXXV. 1913.

Lescuraea radicosa (Mitt.) Mönkem., Die Laubm. Eur. 693. 1927.

Lescuraea radicosa var. *pfundtneri* (Limpr.) Mönkem, Die Laubm. Eur. 693. 155e. 1927.

Pseudoleskea radicosa var. *brachyclados* (Schwägr. *in* Schultes) Podp., Cons.

Musc. Eur. 533. 1954.

Lescuraea radicosa var. *radicosa f. holzingeri* (Best) E. Lawton, Bull. Torr. Bot. Cl. 84(4): 302. 1957.

Nomenclatural notes: Schwägrichen described *Leskea brachyclados* in 1804 for specimens collected by J.A. Schultes at Salmshöhe, Austria. In his description, Schwägrichen commented on the similarity of *Leskea brachyclados* with *Leskeae incurvata* (= *Lescuraea incurvata*), noting these differences. *Leskea brachyclados* has leaves less incurved, serrate, and less secund than in *Leskeae incurvata*, branches more numerous, and operculum non-conic. In 1812, Bridel stated the differences between *Leskea brachyclados* and *L. incurvata* are too weak to be considered at the specific level, and felt they should not be separated. Then in 1816, Schwägrichen listed *Leskea brachyclados* and *L. incurvata δ implexa* as synonyms of *L. incurvata*. Lastly, in 1827 Bridel reduced Schwägrichen's name to the level of variety, as *Leskea incurvata* var. *brachyclados*. It would appear Bruch and Schimper reviewed Schwägrichen's specimens when they described the genus *Pseudoleskea*, placing *Leskea brachyclados* and *Leskea incurvata* var. ß *brachyclados* in synonymy with the newly described *Pseudoleskea atrovirens* (= *Lescuraea incurvata*). Kindberg (1884) raised Schwägrichen's name to the specific level, and made the new combination, *Pseudoleskea brachyclados*. Then in 1885, Kindberg transferred the species to *Lescuraea*. In 1913, Cardot reduced the species to a variety of *Pseudoleskea incurvata*. Thereafter, Schwägrichen's specimen was essentially ignored, when in 1954 Podpera made the new combination *Pseudoleskea radicosa* var. *brachyclados*. Then in 1957, Lawton briefly reviewed Schwägrichen's *Leskea brachyclados*. Although Lawton never viewed any specimens herself, she discussed the name *brachyclados* under *Lescuraea saviana*, stating that De Notaris (1869) believed Schwägrichen's name to be synonymous with the latter. Having examined the tiny Schwägrichen specimen at G, *Leskea brachyclados* is clearly synonymous with *Hypnum radicosum*, as well as being an earlier described name (Fig. 2.37). Even Best (1900) and Culmann (1910) pronounced specimens under the name *Leskea brachyclados* from Schwägrichen's herbarium at G, as *Pseudoleskea radicosa*. However, Culmann (1910) also expressed the opinion that the specific epithet *brachyclados* should be completely abandoned. In a recent checklist, Frey and Kürschner (1991) listed specimens from southwest Asia as *Pseudoleskea brachyclados*. Since *Leskea brachyclados* has not been treated in a revision after 1963, Crosby *et al.* (1999) identified *Pseudoleskea brachyclados* as an insufficiently known taxon. Given that *Leskea brachyclados* is clearly synonymous with *Hypnum radicosum* and is an earlier described name, it has priority over Mitten's *H. radicosum*. However, as the specific epithet *radicosa* is stable and most do not recognise the epithet *brachyclados*, it is not in the best interest of nomenclature to follow priority, as confusion will most likey result. A proposal to conserve the epithet *radicosa* will be made, with recognition of *brachyclados* as an earlier synonym.

Hypnum radicosum was described by Mitten in 1865, using specimens collected and identified by Drummond (no. 225) as *H. tenax*. As discussed previously, Drummond's original collections were mixed, and not until Wilson (1828) reviewed Drummond's collection was this made known. However, Wilson did not give descriptions of the two species he had named. Consequently, both names (*Leskea rigescens* and *Pseudoleskea congesta*) are invalid.

There are four cards (with specimens) affixed to a single herbarium sheet at NY, and filed as '*Hypnum radicosum* type' (Fig. 2.38). It is evident that Mitten reviewed specimens on two of the four cards, as line drawings of leaves, cells, and paraphyllia, as well as notes were made. The specimen in the bottom, right-hand corner (NY 00322420) is designated as the lectotype since the accompanying card exhibits most of Mitten's drawings and hand-written notes. The specimen in the bottom left-hand corner (NY 00322421), although considered the type by Lawton, only exhibits a few drawings and handwritten notes. It is unclear how Lawton chose this specimen as the type, and as such is designated as an isotype. The card in the top, right-hand corner (NY 00322423) contains a small specimen, as well as a packet with Mitten's reproduced drawings from the lectotype. The origin of the small specimen as well as of Mitten's reproduced drawings is unclear given that there is no indication that Mitten reviewed the specimen or produced the print. As a result, I do not feel confident in designating this specimen as an isotype. Similarly, the card in the top, left-hand corner (NY 00322422) contains two specimens, both of which do not appear to have been reviewed by Mitten. The upper specimen is *Lescuraea radicosa*, and the lower specimen is clearly *Lescuraea stenophylla.* In addition, the lower specimen has sporophytes and some plant material of *Hypnum uncinatum* mixed in with it. Since both upper and lower specimens are affixed to the same card, and there is no indication that Mitten reviewed either of them, they are not designated as type material.

Pseudoleskea sciuroides was described by Kindberg and Macoun in 1890, from specimens collected by Dawson in British Columbia, Canada. A single specimen is located at S, and is clearly the holotype.

Limpricht described *Ptychodium pfundtneri* in 1895 from specimens collected by Breidler and by Weber. Unfortunately, only Weber's (27. Juli 1887) specimen was made available on loan from BP. It is unknown whether the syntypes exist, or simply were not provided on loan. Weber's specimen has sporophytes and according to Limpricht, Breidler's specimens are all sterile. For this reason Weber's specimen is chosen as the lectotype. The specimens of Breidler, although not reviewed, are designated as syntypes.

The holotype of *Pseudoleskea bicolor* was described by Kindberg from a specimen collected by Nyman in Sweden. The holotype at S is a large specimen, with the packet information matching the type citation. After having examined the specimen, it became evident how Kindberg came up with the specific epithet 'bicolor'. Where the stems and branches are distinctly brownish-black in colour, only the apices are distinctly greenish-yellow in colour. There is also a smaller specimen at S consisiting of several strands, which appears to have been made when Kindberg made the new combination, *Ptychodium bicolor*, in 1904. This specimen is designated as an isotype.

Pseudoleskea denudata var. *holzingeri* was described by Best in 1900, from specimens collected by Holzinger and Blake near Lake McDonald, as well as from specimens collected by Williams and by Dr. Bell. A specimen at NY (*Williams 343*) with sporophytes is designated as the lectotype. Two specimens of *Willams 343* at F, also with sporophytes, are designated as isotypes. A single sterile specimen at NY collected by Holzinger and Blake, is designated as a syntype. No specimens from Dr. Bell were seen. Crum *et al.* 1900, also consider *P. denudata* var. *Holzingeri* to be synonymous with *Pseudoleskea radicosa* (= *Lescuraea radicosa*).

Lastly, Kindberg described *Pseudoleskea jemtlandica* in 1903 from specimens collected by Adlerz, also in Sweden. There are two specimens at S, the larger of which is the holotype. A small specimen that is clearly a portion of the type is designated as an isotype.

***Lescuraea radicosa sensu lato*:**

Plants small to large-sized, somewhat julaceous and robust, soft and lax, or stiff and robust, forming ± densely intertwining mats or very loose mats or wefts; yellowish to yellow-green, older stems and branches yellow-orange to brown, very old stems devoid of leaves, brown and wiry, or brown and not devoid of leaves, dull or satin-glossy. Stems prostrate, apices slightly to distinctly hooked; distinctly to somewhat fragile when dry; outer cortical cells mostly of 1-2 layers, orange-red, ± thick-walled; cells of medulla thin-walled, rounded, abruptly large-lumened, hyaline; central strand distinct. Branching irregularly; branches numerous and short, to few or lacking, prostrate or erect. Rhizoids smooth; orange-brown; numerous to lacking; ± branching profusely; ± forming densely matted tufts along stems, matted tufts uncommon near stem apex. Paraphyllia multiform, filamentous to foliose, short to long filamentous, distinctly branched; cells thin-walled, quadrate to elongate, ± distinctly prorate; numerous on younger portions of stems and branches, ± lacking on old stems. Stem leaves ± densely arranged; julaceous or erect and appressed when dry, spreading or erect when moist; acumen short and incurved or long and highly flexuose above; distinctly to somewhat concave below; asymmetric to symmetric, not or slightly falcate to distinctly falcate-secund; distinctly biplicate, sometimes numerous longitudinal plicae throughout; narrowly short or long decurrent; ovate and abruptly short acuminate to ovate-lanceolate and gradually long acuminate, acumen distinctly shorter or longer than the leaf proper; 0.65-2.38 mm long x 0.40-1.01 mm wide, mostly 0.85-2.24 mm long x 0.45-0.92 mm wide. Branch leaves similar in shape to stem leaves, usually somewhat smaller. Margins distinctly to slightly serrate at apex, acumen distinctly to slightly serrate; narrowly recurved from lower acumen to leaf base or narrowly recurved from lower acumen to mid-leaf, broadly recurved from mid-leaf to leaf base, sometimes more so on one side, not recurved from upper to lower acumen. Branch leaves similar in shape, usually somewhat smaller. Costa yellowish-green; subpercurrent to distinctly percurrent; stout below, narrowing in acumen; abaxial surface ± keeled; slightly prorate along upper abaxial portion. Laminal cells mostly echlorophyllose, ± translucent. Alar region small to medium, usually extending ¼ up leaf margin; cells ± thin-walled, lax, quadrate, enlarged quadrate to enlarged rectangular, some elongate cells interspersed; 4.8-28.8 µm long x 7.2-16.8 µm wide, mostly 12.0-16.8 µm long x 10.8-14.4 µm wide. Basal cells thin-walled, lax; never pitted or rarely very few slightly pitted cells interspersed; enlarged quadrate to rectangular; 7.2-48.0 µm long x 7.2-16.8 µm wide, mostly 12.0-33.6 µm long x 9.6-12.0 µm wide. Median cells thin-walled, pseudo-pitted; homogeneous within leaf, marginal cells smaller; rhombic, rhomboidal, fusiform or fusiform-linear with ± rounded ends, longer cells ± sinuolate, sometimes few rectangular cells interspersed; 12.0-60.0 µm long x 4.8-12.0 µm wide, mostly 16.8-36.0 µm long x 4.8-9.6 µm wide. Distal cells thin-walled; rhomboidal to fusiform-linear; 9.6-57.6 µm long x 4.8-12.0 µm wide, mostly 14.4-36.0 µm long x 6.0-9.6 µm wide. Papillae round; prorate; distal cells slightly prorate, median cells ± rarely prorate; branch leaves somewhat more distinctly prorate. Perichaetia common to rare, satin and translucent; perichaetial leaves erect, lanceolate, gradually short to long acuminate, somewhat serrate above; clasping seta throughout; costa ± narrow throughout, ± ending in lower acumen, rarely extending as very narrow line into mid-acumen; basal cells lax, rectangular, median cells thin-walled, long fusiform-linear, distal cells thin-walled, short-rhomboidal to fusiform; prorae lacking. Perigonia rare, sometimes several along stems, none seen on branches; perigonial bracts ovate-acuminate, appressed, concave, entire; costa narrow, ending mid-leaf or lacking; basal cells not or slightly lax, rectangular, median cells ± thin-walled, sinuose-fusiform; prorae lacking. Sporophyte rare to common. Seta smooth; yellow-orange to orange-red; dextrorse below, distinctly sinistrorse above; 6.8-15.0 mm long. Capsule slightly arcuate, suberect to nearly erect, cylindric, ± symmetric; orange to orange-brown; rough and dull; constricted below mouth when dry, ± mouth flaring outward, swollen when moist; 1.0-2.0 mm long. Operculum short rostrate to slightly conical. Peristome inserted along mouth of capsule. Exostome teeth orange below, yellow-hyaline above; lanceolate, slightly 'shouldered'; inflexed, distal portions touching endostome segments; joined at base to form an orange-brown band; proximal dorsal surface with fine horizontal papillose-striae ± ⅓ the height of tooth, fine papillose-striae or fine papillae in vertical or oblique pattern in median portion, fine papillae leading to sparse and rounded papillae in distal portion of tooth; apex sharp to somewhat blunt; ventral surface distinctly trabeculate; 264-500 µm long. Endostome segments yellowish-hyaline; as long or somewhat shorter than exostome, rarely broken off; lanceolate, distinctly keeled, straight; narrowly perforate along median line; narrowly spaced, joined to form a medium basal membrane of similar colour ¼ to ⅓ height of segments; dorsal and ventral surfaces somewhat sparse and minutely papillose throughout; 206-372 µm long; cilia ± reduced, 1-2, appendiculate to nodose, minutely papillose. Spores 12.0-24.0 µm in diameter, mostly 16.8-21.6 µm in diameter. N = not reported.

Variation: *Lescuraea radicosa sensu lato* has considerable variation in western North America. However, there are distinct substrate and habitat-driven character states that can be identified. Plants growing on exposed, dry, siliceous boulders and outcrops, tend to be small yet robust in appearance as well as distinctly julaceous and compact. Branches are short, numerous, and crowded along the stem. Rhizoids are numerous, and form continuous tufts along stems. Laminal cells of these compact plants are rhombic, rhomboidal, or rarely short fusiform, and the lumen is slightly 'pseudo-pitted'. The costa is stout below and gradually narrows to the lower or mid-acumen. Sporophytes are occasional. Less exposed, slightly mesic to dry siliceous rocks and boulders tend to have small or medium-sized, soft and lax plants that are not at all julaceous and compact. These plants are usually somewhat falcate, but never distinctly falcate-secund. Branches are short or long and numerous. However, they are rarely crowded along the stem. Rhizoids are also numerous, and form continuous tufts along stems. Laminal cells of these plants are mostly long fusiform, and the cell lumen is distinctly 'pseudo-pitted'. The costa is stout below, and narrows gradually throughout, becoming percurrent. Sporophytes are commonly produced along the stems of these less exposed plants. Lastly, terricolous plants growing under dense canopies of species of *Cassiope*, Poaceae, and other herbs in subalpine meadows, and more commonly in alpine meadows and tundra, tend to be large or very large, distinctly stiff and robust, with falcate-secund leaves. Branches are very rare, but when present, are short and sparsely arranged along the stem. Rhizoids are also very rare, occasionally forming somewhat pendulous strands near stem apices. Laminal cells of these plants are mostly fusiform-linear, and the cell lumen is distinctly 'pseudo-pitted'. The costa is stout throughout, narrowing in the acumen to become distinctly percurrent.

Key to the Infraspecific Taxa of *L. radicosa*

1. Plants large to very large, very robust and stiff; stem apices distinctly hooked; branches and rhizoids few or mostly lacking; paraphyllia mostly long filamentous, prorate and branched; leaves mostly 1.60-2.24 mm long x 0.72-0.92 mm wide, long acuminate, distinctly falcate-secund; laminal cells fusiform to fusiform-linear, alar cells often somewhat prorate; predominantly terricolous beneath heath and herbs in subalpine and alpine meadows or tundra .... ***L. radicosa* var. *denudata*** (p. 109)

1. Plants small to medium, somewhat julaceous and robust, or erect and appressed, soft and lax; stem apices slightly hooked; branches and rhizoids numerous; paraphyllia mostly short filamentous, prorate and slightly branched; leaves mostly 0.85-1.67 mm long x 0.45-0.70 mm wide, short to long acuminate, not or slightly falcate; laminal cells rhombic, rhomboidal, to long-fusiform, alar cells never somewhat prorate; predominantly saxicolous on siliceous rocks, boulders, and outcrops in subalpine forests or in exposed subalpine to alpine meadow 2

2. Plants mostly small, somewhat robust and julaceous; branches crowded along stems; leaves mostly 0.85-1.34 mm long x 0.45-0.53 mm wide, short to slightly long acuminate; laminal cells mostly rhombic, rhomboidal, to fusiform; saxicolous on exposed rocks, boulders, and outcrops in subalpine to alpine meadows ....
.... ***L. radicosa* var. *compacta*** (p. 105)

2. Plants mostly medium, soft and lax; branches not crowded; leaves mostly 1.30-1.67 mm long x 0.50-0.70 mm wide, long acuminate; laminal cells mostly long fusiform; saxicolous on rocks and boulders in subalpine forests ....
.... ***L. radicosa* var. *radicosa*** (p. 100)

L. radicosa **(Mitt.) Mönkem. var.** ***radicosa***

Description: Plants small to medium-sized, soft and lax, forming loose or somewhat densely intertwining mats; yellow-green to light green, older stems and branches somewhat brown, satin-glossy. Stem apices slighty hooked; distinctly fragile when dry; outer cortical cells of 1-2 layers. Branching: branches ± numerous and short. Rhizoids numerous, branching profusely; forming densely matted tufts along stems. Paraphyllia mostly somewhat long filamentous, somewhat branched and prorate. Stem leaves somewhat densely arranged; erect and appressed when dry, erect to spreading when moist; somewhat concave below; not or somewhat falcate; biplicate; narrowly long decurrent; ovate-lanceolate, rarely lanceolate; gradually long acuminate, the acumen as long or somewhat longer than the leaf proper, rarely somewhat shorter; 1.10-1.75 mm long x 0.44-0.94 mm wide, mostly 1.30-1.67 mm long x 0.50-0.7 mm wide (rarely greater than 1.75 mm long). Margins of acumen distinctly serrate due to long marginal cells. Alar cells 4.8-24.0 µm long x 7.2-16.8 µm wide, mostly 9.6-16.8 µm long x 12.0-14.4 µm wide (rarely greater than 21.6 µm long). Basal cells never pitted; 9.6-40.8 µm long x 7.2-16.8 µm wide, mostly 14.4-26.4 µm long x 9.6-12.0 µm wide (rarely greater than 31.2 µm long). Median cells rhomboidal to fusiform-linear with rounded ends, sometimes rectangular cells interspersed; 16.8-60.0 µm long x 4.8-12.0 µm wide, mostly 21.6-36.0 µm long x 7.2-9.6 µm wide (rarely greater than 43.2 µm long). Distal cells rhomboidal below, becoming fusiform-linear above; 12.0-57.6 µm long x 4.8-12.0 µm wide, mostly 21.6-36.0 µm long x 7.2-9.6 µm wide (rarely greater than 38.4 µm long). Perichaetia common. Perigonia rare. Sporophyte common. Seta 6.8-15.0 mm long. Capsule 1.0-2.0 mm long. Exostome teeth 264-500 µm long. Endostome segments 206-372 µm long. Spores 12.0-24.0 µm in diameter, mostly 16.8-21.6 µm in diameter.

Diagnostic characters: *Lescuraea radicosa* var. *radicosa* is distinguished by: 1) its soft and lax plant habit; 2) lanceolate and gradually long acuminate leaves; 3) numerous short, uncrowded, prostrate or sometimes erect branches; 4) highly branched rhizoids, forming extensive matted tufts along stems; 5) leaves mostly erect, appressed, and symmetric; 6) an acumen as long or often somewhat longer than the leaf proper; 7) laminal cells rhomboidal-fusiform to fusiform-linear, thin-walled and distinctly pseudo-pitted; 8) distal and some median cells slightly prorate; 9) paraphyllia short filamentous and prorate, slightly branched below; and 10) predominantly saxicolous on siliceous rocks and boulders in diffusely-lit subalpine forests.

Lescuraea radicosa var. *radicosa* is distinctly intermediate between var. *compacta* and var. *denudata* in most of its character states, as well as being the most common. As indicated previously, this same trend of 'small and compact', 'intermediate', and 'large' plants also occurs in *L. incurvata sensu lato*. Although the range in leaf size of *L. radicosa* var. *radicosa* does overlap with the upper and lower leaf sizes of var. *compacta* and var. *denudata* respectively, leaf shape including the attributes of the laminal cells, are limited mostly to this variety.

Lescuraea radicosa var. *radicosa* can often appear similar to *Lescuraea stenophylla* in general appearance, leaf shape, long acumen, and laminal cells. However, the sporophyte of the former is never as reduced as in the latter. *Lescuraea stenophylla* has distinctly terete endostome segments, as well as a very low basal membrane and no cilia. *Lescuraea radicosa* var. *radicosa* has distinctly keeled segments, a medium to low basal membrane, and somewhat reduced cilia.

Lescuraea radicosa var. *radicosa* is often confused with *L. incurvata* var. *incurvata*. However, the distinctly thin-walled and relatively homogeneous laminal cells in the former, with its distinctly 'pseudo-pitted' cell lumen, reliably separate it from the latter. Where the cell walls are very thick in *L. incurvata*, resulting in cell lumens that appear elliptic, cell walls in *L. radicosa* are thin-walled, and take on a rhomboidal-fusiform to fusiform-linear appearance. Besides being thinner-walled, the laminal cells of *L. radicosa* var. *radicosa* are on average longer and wider than in *L. incurvata* var. *incurvata*. In addition, where most alar cells are distinctly transversely elongate or transversely rectangular in *L. incurvata* var. *incurvata*, alar cells are distinctly enlarged quadrate to enlarged elongate in *L. radicosa* var. *radicosa*.

Variation: Most of the variation in *Lescuraea radicosa* var. *radicosa* is in leaf length and width, being 1.10-1.75 mm long x 0.44-0.94 mm wide (usually 1.30-1.67 mm wide), with laminal cell shape mostly homogeneous. Cell length tends to be homogeneous within but often variable between specimens.

Habitat: *Lescuraea radicosa* var. *radicosa* occurs predominantly on moist, shaded rocks and boulders in subalpine *Abies-Pseudotsuga* forests, as well as on soil-accumulated rock outcrops in somewhat more exposed areas. It is not exclusive to these substrata or forest types. This taxon sometimes grows on bark at the bases of *Abies* sp. or *Populus* sp. trees or on humus in moist woods. Elevation: approximately 685-3200 metres (mostly 1800-3000 m, rarely less than 1500 or greater than 3020 m).

Distribution: *Lescuraea radicosa* var. *radicosa* is very common in North America and has been collected from north- and southwestern and southeastern British Columbia, including Vancouver Island; Jasper, Banff, and Waterton Lakes National Parks in Alberta; southernYukon territory; the Alexander archipelago in Alaska; Washington; Oregon; the northern portion of California; central Idaho; northwestern and southcentral Montana; northwestern and southeastern Wyoming; and Colorado. Single collections have been made in Osier Island, Alaska; Utah; and New Mexico. It is disjunct in eastern North America in the Keeweenaw Peninsula, Michigan; White Mountains of New Hampshire; Gaspé Co., Québec, Newfoundland, and Labrador. Some collections from Labrador are *L. saxicola* and not *L. radicosa* var. *radicosa*. *Lescuraea radicosa* var. *radicosa* is also known from Greenland, Europe, the Near East, and East Asia.

Specimens examined: **ASIA:** **INDIA:** **Kashmir:** Gulmarg – *Stewart 15531* (F). **EUROPE:** **AUSTRIA:** Glockner: Salmshöhe – *Schultes* (G – lectotype of Leskea brachyclados). **CZECH REPUBLIC:** **Bohemia:** Montes Krkonoše – (F). **FRANCE:** Dep. des Hautes Alpes: lac de la Douche – *Culmann 5969* (MO). **SWEDEN:** Jämtland: Storlien – *Adlerz* anno 1882 (S – holotype of Pseudoleskea jemtlandica, S – isotype). Lapland: near Lake Virijaur – *Nyman* anno 1893 (S – holotype of Pseudoleskea bicolor, S – isotype). **SWITZERLAND:** Eggischhorn Wallis – *Weber* 27. Juli 1887 (BP – lectotype of Ptychodium pfundtneri). **NORTH AMERICA:** **CANADA:** **Alberta:** Banff National Park: Moraine Lake – *Crum & Schofield 3935* (MICH), *Krieger & Krieger 1486, 1487, 1488, 1500* (ALTA), *Krieger & Hebben 1878, 1879, 1880, 1881, 1882, 1883, 1884, 1885* (ALTA), Lake Agnes – *Krieger & Hebben 1900* (ALTA), Peyto Lake – *Crum & Schofield 5170* (MICH). Bow River Watershed: Highwood Pass – *Bird & Glenn 13626* (UBC). Jasper National Park: Tonquin Valley – *MacFadden* (MO), Mt. Edith Cavell – *Krieger 1740, 1742* (ALTA). Kananaskis Country: Highwood Pass –

Krieger 1706, 1715, 1726 (ALTA), Plateau Mtn – *Krieger 1719* (ALTA). SW of Lethbridge: Belly River – *Bird 3623* (CANM). Mountain Park Area: Mtn Park Summit – *Vitt & Peterson 6943* (UC/JEPS). Waterton Lakes National Park: Cameron Lake – *Hermann 20581* (WTU), *Crum & Schofield 5678* (MO). Wilmore Wilderness Area: Hardscrabble Pass – *Krieger 1783* (ALTA). **British Columbia:** Black Tusk Area: near campground – *van Velzen & Leong 262* (UBC). Bugaboo Provincial Park: Cobalt Lake – *Tan & Ensing 77-1777* (UBC). Cassiar Mtns: Atsulta Range – *Schofield 65877 1* (UBC). Glacier National Park: *MacFadden 17784* (MO), Loop Creek Campground – *Krieger & Hebben 1870, 1871, 1874* (ALTA). Kokanee Glacier Park: Gibson Lake – *Schofield & Jamieson 59049* (UBC). Monashee Mtns: Malton Range – *Vitt 34224* (ALA). North Vancouver: Mt. Seymour – *Ireland 6010* (WTU). Portage River – *Drummond 225* (NY – lectotype of Hypnum radicosum, NY – isotype). Prince George Forest Region: N. of Star Mtn – *Ketcheson & Meidinger M310-7* (UBC). Rocky Mts: Valley of Elk River – *Dawson* anno1883 (S – holotype of Pseudoleskea sciuriodes). Sandon: *MacFadden 4222* (MO). Selkirk Mts: Roger's Pass – *Macoun 627* (MO). Vancouver Island: Burman Lake area – *Boas 122* (UBC), Strathcona Provincial Park: Marble Meadows – *Halbert 7837* (UBC). Wells Gray Provincial Park: Hemp Creek Ranger Station – *Ahti 15489* (UBC). near Wilmer: Lake of Hanging Glaciers – *MacFadden 4219* (MO). Whistler Mtn – *van Velzen & Leong 302.80607* (UBC). **Labrador:** Battle Harbor – *Waghorne* (NY). Cape Charles – *Waghorne 41* (FH). **Newfoundland:** North District: Griquet Harbour – *Belland, Schofield & Jamieson 11078* (UBC), White Bay: Cremaillere Harbour – *Fife 2013* (MICH, NY). **Quebec:** Gaspé Co.: Mt. Albert – *Allen* (NY). **Yukon:** Lake Lindeman – *Williams* (F, MO). Selwyn Mts: Itsi Range – *Schofield, Vitt & Horton 70211* (UBC). on border to Northwest Territories: Howard Pass – *Rosie 164* (CANM). **GREENLAND:** Angmagssalik District: Ikateq – *Lewinsky 71-207* (ALA). Gothåb District (NY). Ilimaussaq Peninsula: Angnikitsoq, Drynæs (NY). Kangerdlugssuaq District (NY). Sklodungen District (NY). **USA: Alaska:** Alexander Archipelago: Osier Island: Russel Fjord – *Mazaika 5266* (MICH). Alaska Peninsula: Aniakchak National Monument: Aniakchak Caldera – *Hasselbach* (ALA). E of Alaska Peninsula: Kodiak Island – *Mylroie 16* (NY). **California:** Del Norte Co.: near Doctor Rock – *Norris 50319* (UC/JEPS). Sierra Co.: E. of Yuba Pass – *Lawton 3131* (WTU). Siskiyou Co.: Sawyer's

Bar Road – *Hermann 24802* (WTU). Tehama Co.: North Yolla Bolly Mtn – *Norris 57501* (UC/JEPS). **Colorado:** Boulder Co.: Fawnee Pass Trail – *Hermann 24086* (WTU). Eagle/Summit Co.: Junction of Acapaho & White River National Forests – *Young 29* (WTU). Garfield Co.: *Churchill 78323* (MICH). Gilpin Co.: Jenny Lind Creek – *Grout 466* (MO). Gunnison Co.: NW of Schofield Pass – *Weber 9223* (WTU). Larimer Co.: Mill Creek Basin – *Hermann 26008* (MICH). Mesa Co.: Mesa Lakes – *Hermann 26514* (F). Mineral Co.: San Juan Mts – *Hermann 23343* (WTU). Pitkin Co.: W. of Buttermilk – *Matthews 1130* (FH). **Idaho:** Custer Co.: Sawtooth Wilderness Area – *Morton 8526* (WTU). Elmore Co.: Boise National Forest – *MacFadden 17778* (UBC). Valley Co.: Ponderosa State Park – *Hermann 20281* (WTU). Traille Rim Basin – *Leiberg 220* (MO). **Michigan:** Keeweenaw Co.: Ahmeek Area – *Janssens 7325* (WTU), Dow Wilderness Area – *Trynoski 34* (MICH). Ontonagon Co.: Government Peak – *Darlington 295* (NY). **Montana:** Columbia Falls: *Williams 343* (NY – lectotype of Pseudoleskea denudata var. Holzinger, F – isotype (2 specimens)). Flathead Co.: near Lake McDonald – *Holzinger & Blake* (NY – syntype of Pseudoleskea denudata var. Holzinger, FH – isotype). Glacier Co.: Glacier National Park: St. Mary Valley – *Hermann 20435* (MICH), Two Medicine Lake – *Hermann 20448* (MICH). Lake Co.: Mission Mts – *McCune 3874* (OSC). Sweetgrass Co.: Big Timber Falls – *Vitt & Hastings 35513* (MO). **Nevada:** Ormsby Co.: E. of Lake Tahoe – *Lawton 3101* (NY). **New Hampshire:** White Mts: Tuckerman's Ravine – *Allen 399* (CANM). **New Mexico:** Taos Co.: Sangre de Cristo Mts – *Hermann 23968* (WTU). **Oregon:** Baker Co.: Cornucopia – *Young 704* (WTU). Clamath Co.: Crater Lake National Park – *Young 579* (WTU). Hood River Co.: Mt. Hood – *Lawton 4417* (WTU). Jackson Co.: S. of Ashland – *Allen 703* (MO). Umatilla Co.: Blue Mts – *Flowers 3853* (NY). **South Dakota:** Lawrence Co.: Black Hills – *Churchill 8911* (MO). **Utah:** Salt Lake Co.: Lamb's Canyon – *Flowers 2500* (WTU). **Washington:** Chelan Co.: Chelan Mts – *Hermann 19044* (MICH). King Co.: White River – *Grant* (WTU). Pierce Co.: Mt. Rainer – *Lawton 3317* (OSC). Port Angeles – *Hartill 43* (FH). **Wyoming:** Albany Co.: Medicine Bow Mts – *Hermann 17742* (WTU). Park Co.: Bear Tooth Butte – *Lawton 1943* (WTU). Teton Co.: Grand Teton National Park – *Duell 2261/2* (F), SE of Vector – *Duell 2225/2* (F). Yellowstone National Park – *Lawton 1904* (WTU).

***L. radicosa* var. *compacta* (Best) E. Lawton,** Figure 2.41-2.43

Bull. Torr. Bot. Cl. 84: 305. 1957.

Pseudoleskea radicosa var. *compacta* Best, Bull. Torr. Bot. Cl. 27: 231. f.7. 1900. **Type:** "On rocks, Rocky Mts., B.C., Professor Macoun." **Holotype – NY !; isotypes – NY !** (2 specimens)

Pseudoleskea pallida Best, Bull. Torr. Bot. Cl. 27: 227. f.6. 1900. ***synon. nov.*** **Type:** "Type locality Colorado; type in coll. of Columbia University; Collected by T.S. Brandegee." **Holotype – NY !**

Pseudoleskea congesta Bruch & Schimp. *in* B.S.G *ex* Paris var. *compacta* (Best) Par., Ind. Bryol. ed. 2, 4: 103. 1905.

Lescuraea radicosa var. *pallida* (Best) E. Lawton, Bull. Torr. Bot. Cl. 84: 306. 1957.

Pseudoleskea radicosa var. *pallida* (Best) Crum, Steere & Anderson, Bryologist 67: 164. 1964.

Nomenclature: *Pseudoleskea radicosa* var. *compacta* was described by Best in 1900, from specimens collected by Macoun at Roger's Pass, British Columbia on July 31, 1890. Best was conscientious in identifying type material, and the three specimens at NY are clearly type material. On the first packet at NY, Best indicated that the specimen is a portion of the type from Canadian Musci 340, in the collection of the Geological Survey. Best also revealed that this is a new variety, as well as writing 'type'on the label. This specimen is clearly the holotype. Macoun's collection at the Geological Survey of Canada has been incorporated into CANM. Unfortunately, the CANM specimen has not been examined. The other two packets at NY have 'from type specimen' and 'portion of type', respectively on the packet labels. Examination of both specimens reveals mineral soil identical to that of the holotype, supporting the view that they are from the same collection. These two specimens are designated as isotypes.

Pseudoleskea pallida was also described by Best in 1900, from specimens collected by Brandegee within 100 miles of Canyon City, Colorado, 1874-1878. There are two packets at NY, and only one has the word 'type' clearly identified on the packet label. This specimen is the holotype. There is no indication that the specimen in the second packet is type material, and an examination of the compact specimen refutes the idea that it could be type material. Where stem and branch apices of the holotype are yellow-green in colour, they are distinctly orange-yellow in this second specimen. This specimen is clearly *Lescuraea incurvata*. In the revision of *Pseudoleskea* by Best (1900), *P. pallida* was described before *P. radicosa* var. *compacta*, and as such would have priority over the name *compacta*, if placed in synonymy. However, the International Code of Botanical Nomenclature (2000) does not indicate rules of priority within the same article. Following examination of a number of specimens within both taxa, it quickly became evident that the name *compacta*, more aptly describing the physical characteristics of the plant, is considerably more appropriate. Specimens identified as *P. pallida* (including the type) do not appear very 'pallid'. More importantly, these specimens cannot be differentiated from *P. radicosa* var. *compacta*. For these reasons, the name '*compacta*' is retained, and *P. pallida* is placed in synonymy.

Description: Plants small-sized, julaceous and somewhat robust, forming densely intertwining mats; apices yellow-green, light green to green, remainder of stems and branches yellow-brown to brown, somewhat dull. Stem apices slighty hooked; distinctly fragile when dry; outer cortical cells of 1-2 layers. Branching: branches numerous and short, crowded along stem. Rhizoids ± numerous, branching profusely; sometimes forming densely matted tufts along stems. Paraphyllia mostly short filamentous and somewhat branched. Stem leaves densely arranged; julaceous and appressed when dry, erect to spreading when moist; the short or somewhat long acumen slightly incurved or erect; concave below; mostly asymmetric, not or rarely somewhat falcate; usually biplicate; narrowly short decurrent; ovate-acute to ovate-lanceolate, abruptly short or gradually long acuminate, often both on single stem; the acumen distinctly shorter or rarely as long as the leaf proper; 0.65-1.55 mm long x 0.40-0.71 mm wide, mostly 0.85-1.34 mm long x 0.45-0.53 mm wide (rarely greater than 1.45 mm long). Margins of acumen distinctly serrate due to short marginal cells. Costa subpercurrent to ± percurrent; stout below, narrowing slightly in lower acumen; abaxial surface distinctly keeled; ± distinctly prorate along upper abaxial portion. Laminal cells sometimes chlorophyllose and slightly opaque. Alar cells 4.8-21.6 μm long x 7.2-16.8 μm wide, mostly 12.0-16.8 µm long x 10.8-13.2 µm wide (rarely greater than 16.8 µm long). Basal cells 7.2-33.6 µm long x 7.2-16.8 µm wide, mostly 12.0-21.6 µm long x 9.6-12.0 µm wide (rarely greater than 28.8 µm long). Median cells slightly pseudo-pitted; rhombic, rhomboidal to fusiform; 12.0-40.8 µm long x 4.8-12.0 µm wide, mostly 16.8-28.8 µm long x 7.2-8.4 µm wide (rarely greater than 36.0 µm long). Distal cells rhomboidal below, becoming ± fusiform above; 9.6-36.0 µm long x 4.8-12.0 µm wide, mostly 14.4-28.8 µm long x 7.2-8.4 µm wide (rarely greater than 33.6 µm long). Perichaetia and Perigonia occasional. Sporophyte rare. Seta 7.0-8.0 mm long. Capsule 1.0-2.0 mm long. Exostome teeth 300-335 µm long. Endostome segments 220-235 µm long. Spores 12.0-21.6 µm in diameter, mostly 16.8-19.2 µm in diameter.

Diagnostic characters: *Lescuraea radicosa* var. *compacta* is distinguished by: 1) its julaceous and 'compact' plant habit, although some stem and branch leaves appear more like var. *radicosa*; 2) ovate and abruptly acuminate leaves, sometimes gradually acuminate; 3) numerous, often crowded branches; 4) leaves distinctly to somewhat incurved, with the acumen also incurved; 5) an acumen shorter than the leaf proper; 6) laminal cells rhombic, rhomboidal, or rhomboidal-fusiform, thin-walled, and somewhat pseudo-pitted; 7) distal and few median cells slightly prorate; 8) paraphyllia short-filamentous, prorate, and slightly branched below; and 9) predominantly saxicolous on siliceous rocks, boulders, and outcrops in alpine areas.

Lescuraea radicosa var. *compacta* is the compact form of the species, with var. *radicosa* and var. *denudata*, repsectively intermediate and large. Although the range in leaf and laminal cell sizes overlaps with lower leaf and laminal cell sizes of var. *radicosa*, leaf shape, including the attributes of the acumen, are mostly limited to this variety. However, *L. radicosa* var. *compacta* sometimes resembles var. *radicosa*. Often, leaves that are clearly of var. *radicosa* can be found among the more compact leaves on plants of var. *compacta*, indicating that both are, but varieties of a single species.

Lescuraea radicosa var. *compacta* may be confused with *L. incurvata* var. *tenuiretis*, since both are saxicolous and compact plants found predominantly in exposed areas. Due to smaller laminal cell sizes, cell wall thickness in the former species may be somewhat harder to ascertain. However, the pseudo-pitted nature, as well as the relatively homogenous laminal cells of *L. radicosa* var. *compacta*, reliably separates it from *L. incurvata* var. *tenuiretis*. In addition, where median and distal cells are mostly rhombic to rhomboidal-fusiform and scarcely prorate in the former taxon, they are distinctly irregular in shape, angular, and the lumens extend obliquely into the prorae in the latter. Besides being thinner-walled, the laminal cells of *L. radicosa* var. *compacta* are on average longer and wider than in *L. incurvata* var. *tenuiretis*. In addition, where most alar cells are distinctly transversely elongate or transversely rectangular in *L. incurvata* var. *tenuiretis*, alar cells are distinctly enlarged quadrate to enlarged elongate in *L. radicosa* var. *compacta*.

Variation: Most of the variation in *Lescuraea radicosa* var. *compacta* is in leaf length and width, 0.65-1.55 mm long x 0.40-0.71 mm wide, mostly 0.85-1.34 mm long x 0.45-0.53 mm wide (rarely greater than 1.45 mm long), with laminal cell shape mostly homogeneous. Cell length and width tends to be homogeneous within, but often variable between specimens.

Habitat: *Lescuraea radicosa* var. *compacta* occurs predominantly on rock outcrops in alpine meadows as well as on rock at treeline. It is sometimes found on rock in open woods. Very rarely is it found on rock in streams or in brooks, often in areas of higher elevation. Elevation: approximately 980-3120 metres (mostly 1800-3050 m).

Distribution: *Lescuraea radicosa* var. *compacta* is not very common in North America. It has been collected from southwestern and southeastern British Columbia; Jasper and Waterton Lakes National Parks in Alberta; southernYukon territory; Idaho; Oregon; northwestern Wyoming; Colorado; Utah; and Arizona. It is disjunct in eastern North America in Gaspé, Quebec as well as in Labrador. Many collections identified as *Pseudoleskea pallida* from Arizona are in fact *Pseudoleskeella arizonae*. *Lescuraea radicosa* var. *compacta* is also known from Norway, and possibly from Europe.

Specimens examined: NORTH AMERICA: CANADA: Alberta: Jasper National Park: Wilcox Pass: near Mt. Athabasca – *Lawton 1415* (WTU), Tonquin Valley – *MacFadden* (MO). Kananaskis Country: Highwood Pass – *Krieger 1707, 1721* (ALTA), Plateau Mtn

– *Krieger 1721* (ALTA). Waterton Lakes National Park: Bertha Lake – *Crum & Schofield 6011* (CANM), *Crum & Schofield 5991* (US). Wilmore Wilderness Area: E. of Hardscrabble Pass and S. of Cavass – *Krieger 1749, 1766* (ALTA), Hardscrabble Pass – *Krieger 1785* (ALTA). **British Columbia:** near Kamloops, Drain Lake – *Brinkman 354* (US). Kootenay National Park: Hector – *Macoun* (MICH). Wilmer, Paradise Mines – *MacFadden 1084* (UBC), *MacFadden 1107* (MO (2 specimens), NY). Selkirk Mts: Roger's Pass – *Macoun 340* (NY – holotype of Pseudoleskea radicosa var. compacta, NY – isotypes (2 specimens)). Silverton: Fisher Maiden Lake – *MacFadden 629* (MO). **Labrador:** Cape Charles – *Waghorne* (NY). **Quebec:** Gaspé Peninsula: Mont Jaques Cartier – *LeBlanc 6746* (WTU). **Yukon:** Kluane National Park: Goatherd Mtn. – *Douglas & Douglas 6998* (WTU). **USA: Arizona:** Coconino Co.: San Francisco Peak – *Haring 11714* (WTU), *Haring & Wetherill 11826* (CANM). **Colorado:** near Canyon City – *Brandegee 73* (NY – holotype of Pseudoleskea pallida). Gunnison Co.: Gothic Natural Area – *Weber 9116* (WTU). Mesa Co.: Mesa Lakes – *Hermann 26516* (NY). **Montana:** Glacier National Park: *Jones 10990* (WTU). **Oregon:** Lane Co.: Little Brother Mtn – *van Veckten* (WTU). **Utah:** Juab Co.: Deep Creek Mtns – *Flowers 5812* (COLO). San Juan Co.: La Sal Mts – *Flowers 2829* (WTU). **Wyoming:** Teton Co.: Cascade Trail – *Lawton 1746* (WTU). Teton National Park: b/w Jenny Lake and Lake Solitude – *Welch 16285* (NY).

L. radicosa* var. *denudata (Kindb. *in* Macoun) E. Lawton, Bull. Torr. Bot. Cl. 84: 302. (annotation: *Lescuraea radicosa* var. *denudada*) Figure 2.44-2.46

Pseudoleskea sciuroides var. *denudata* Kindb. *in* Macoun, Cat. Can. Pl. 6: 181. 1892. **Type:** "On rocks along the Asulcan Creek near the glacier of that name, Selkirk Mountains, B.C., alt. 6,000 feet, August 7th, 1890. (*Macoun*)." [*Macoun 374*; Canadian Musci, No. 564] **Lectotype – S !** (lectotypus); **isotypes – S !** (3 specimens), **UC/JEPS !, NY !, MICH !, F !, MO !, US !** (2 specimens)

Ptychodium oligocladon Limpr., Die Laubm. 2: 801. 1895. (annotation: *Ptychodium oligocladum*). **Type:** "Salzburg: in einer Felsschlucht am Balonspitz bei Zederhaus im Lungau 2500 m, ♀ Exemplare (J. Breidler am

24. Juli 1885), Stubenkogel bei Mittersill 2200 bis 2530 m, ♀ Exemplare (J.Breidler im August 1879), Unter-Sulzbachthal im Pinzgau 2300 m, ♀ Exemplare (J. Breidler am 16. August 1879). – Nur mit Reserve sind ♂ Exemplare von einer Quelle am Rotheck in der Kraggau im Steiermark bei 2600 m (Breidler am 17. Juli 1881) dieser Art zuzurechnen." **Lectotype – BP !** (*Breidler* 24. Juli, 1885, lectotypus); **syntypes – BP !** (*Breidler* August 1879, 2 specimens), (*Breidler* 16. August, 1879), (*Breidler* 17. Juli, 1881)

Pseudoleskea breidleri Kindb., Eur. & N.Am. Bryin. (Mosses) 1: 54. 1897. **Type:** " – Rocks in higher alp. region r. – *Eur.* Salzburg: Breidler: Limpricht." **Holotype – S** (not seen)

Pseudoleskea hyperborea C. Müll. *in* Kindb., Eur. & N.Am. Bryin. (Mosses) 1: 52. 1897. *Fide* Wijk *et al.* 1967. **Type:** "—Arctic district r. *Eur.* Norway near Nord-Cap 1892: W. Baur, com. C. Mueller." **Holotype – S** (not seen)

Pseudoleskea denudata (Kindb. *in* Macoun) Best, Bull. Torr. Bot. Cl. 27(5): 229. 1900.

Pseudoleskea radicosa var. *denudata* (Kindb. *in* Macoun) Wijk & Marg., Taxon 9: 191. 1960.

Nomenclature: *Pseudoleskea sciuroides* var. *denudata* was described by Kindberg from specimens collected by Macoun in the Selkirk Mountains of British Columbia, and listed as Canadian Musci No. 564. There are four packets at S, all with the designation 'ISO-TYPUS', handwritten in pencil. Of the four packets that are loosely affixed to the herbarium sheet, the upper right-hand packet is chosen as the lectotype based on several criteria. There is a label within this packet, indicating the locality, collector, collection date, as well as a Latin diagnosis. The somewhat large specimen is affixed to a small card, with Macoun's collection no., 374, handwritten in ink. There is also a smaller envelope within the packet, containing several loose strands, including a permanent slide. The remaining three packets at S all contain smaller specimens that are clearly from the same initial collection. These are designated as isotypes. Specimens examined at F, MICH, MO, NY, UC/JEPS, and US are designated as isotypes.

Limpricht described *Ptychodium oligocladum* from specimens collected solely by Breidler between 1879 and 1885 in Salzburg and Steiermark, Austria. Of the four syntypes received from BP, three are female while the fourth is a male specimen. However, none of the female specimens displayed any sporophytes. Of the female specimens, only specimen collected by Breidler in Lungau (24. Juli 1885) was large enough to fully display the growth- and lifeforms. The remaining two female specimens consisted merely of several loose strands. Since sporophytes are lacking in all specimens, the larger female specimen is chosen as the lectotype.

Pseudoleskea hyperborea was described by Carl Müller from specimens collected by Baur near Nord-Cap, Norway, in 1892. Unfortunately, type material has not been made available from S.

Description: Plants medium to large-sized, stiff and robust, forming very loose mats or wefts; yellowish to yellow-green, older stems and branches yellow-orange to brown, very old stems devoid of leaves, brown and wiry, satin-glossy. Stem apices distinctly hooked; somewhat fragile when dry; outer cortical cells mostly of 2 layers. Branching: branches very few and short or lacking. Rhizoids few or lacking; branching somewhat; matted tufts rare along stem, when present then matted tufts near stem apex. Paraphyllia mostly long filamentous and distinctly branched; distinctly prorate; distinctly lacking on old stems. Stem leaves densely arranged; erect and appressed when dry or moist; acumen long, becoming highly flexuose above; somewhat concave below; asymmetric, distinctly falcate-secund; distinctly biplicate or numerous longitudinal plicae throughout; narrowly long decurrent; ovate-lanceolate, gradually long acuminate, the acumen as long or longer than the leaf proper; 1.42-2.38 mm long x 0.52-1.01 mm wide, mostly 1.65-2.24 mm long x 0.72-0.92 mm wide (rarely greater than 2.2 mm long, often leaves less than 1.5 mm long mixed in with predominantly larger leaves). Margins of acumen slightly serrate due to very long marginal cells. Alar region medium, usually extending more than ¼ up leaf margin; cells thin- or somewhat thick-walled; 7.2-28.8 μm long x 7.2-16.8 μm wide, mostly 12.0-16.8 μm long x 12.0-14.4 μm wide (rarely greater than 24.0 μm long).

Basal cells rarely thicker-walled and slightly pitted; 9.6-48.0 µm long x 7.2-16.8 µm wide, mostly 16.8-33.6 µm long x 10.8-12.0 µm wide (rarely greater than 36.0 µm long). Median cells fusiform to fusiform-linear with ± rounded ends, somewhat sinuolate or vermicular; 16.8-50.4 µm long x 4.8-9.6 µm wide, mostly 21.6-36.0 µm long x 4.8-7.2 µm wide (rarely greater than 45.6 µm long). Distal cells fusiform-linear; 14.4-52.8 µm long x 4.8-9.6 µm wide, mostly 21.6-36.0 µm long x 6.0-7.2 µm wide (rarely greater than 38.4 µm long). Perichaetia and Perigonia rare. Sporophyte rare; only 2 seen. Seta 6.8-15.0 mm long. Capsule 1.0-2.0 mm long. Exostome teeth not measured. Endostome segments not measured. Spores not seen.

Diagnostic characters: *Lescuraea radicosa* var. *denudata* is distinguished by: 1) its stiff and robust plant habit; 2) very few short branches, or branches mostly lacking; 3) long, ovate-lanceolate and gradually long acuminate leaves; 4) leaves mostly erect, appressed, and distinctly falcate-secund; 5) leaves distinctly biplicate, or numerous longitudinal plicae throughout; 6) laminal cells mostly fusiform-linear, thin-walled, somewhat sinuose or vermicular, and slightly pseudo-pitted; 7) not or indistinctly prorate distal cells; 8) paraphyllia long filamentous, prorate, and distinctly branched below; 9) rhizoids few or lacking; and 10) predominantly terricolous among *Cassiope* sp., in alpine meadows.

Lescuraea radicosa var. *denudata* is the large form of the species, with var. *compacta* and var. *radicosa*, respectively small and intermediate. Many specimens of *L. radicosa* var. *denudata* are consistently larger, and have stem leaves that are larger than in var. *radicosa*. However, some specimens have highly variable stem leaves, even within the same stem section. Where some leaves clearly match the description for var. *denudata*, others belong to var. *radicosa*. Lawton (1957) suggested the difference between var. *radicosa* and var. *denudata* is in leaf size and in the frequency of branches and rhizoids. Where var. *radicosa* is said to have somewhat falcate stem leaves that are ≤ 1.6 mm in length, as well as many branches and rhizoids; var. *denudata* has distinctly falcate-secund stem leaves that are ≥ 1.7 mm in length, as well as very few branches and rhizoids (Lawton 1957). After having examined numerous specimens, Lawton's deliniation between the two varieties appears to be quite accurate. However, as indicated previously, a number of specimens examined appear to be intermediate between the two, with stem leaves ranging from ≤ 1.6 mm to well beyond 2.3 mm in length. Examination of habitat and substrate information from specimens of var. *radicosa* and var. *denudata*, reveal differences that explain the characteristics seen. It appears that saxicolous specimens in subalpine or montane forests have numerous rhizoids and branches, permitting them to adhere to the rock surface. Terricolous specimens, found beneath dense canopies of *Cassiope* sp. and other herbs in alpine meadows and tundra, have very few rhizoids and branches, since they do not have this requirement. The herbaceous cover in meadows and in alpine tundra is quite dense. However, *L. radicosa* var. *denudata* florishes as extensive mats or even wefts beneath the canopy of leaves, such that most of the tundra soil is actually inhabited by this variety. Alpine tundra and meadows often have late snowbeds, releasing moisture gradually. This moisture, in combination with the protective nature of the herbaceous canopy, presumably permits this variety to flourish. In addition, sporophyte production is generally reduced when plants are growing under favourable conditions. Consequently, the lack of sporophytes in var. *denudata* tends to support this observation.

As indicated earlier, some specimens are distinctly variable, with some portions of the plant matching the description of *Lescuraea radicosa* var. *radicosa*, and other parts matching the description of *Lescuraea radicosa* var. *denudata*. Many of these specimens were collected in the narrow zone found between the subalpine forest and alpine tundra. Since the transition between these two zones is rather abrupt, fewer specimens were seen with these shared characteristics. Habitat and substrate differences, as well as shared characteristics, appear to support the distinction of three varieties (and not species) within *L. radicosa*.

Lescuraea radicosa var. *denudata* may potentially be confused with the European taxon *Ptychodium plicatum*, due to their similarity in size, leaf and laminal cell shape, and sporophyte characteristics. Although this taxon has not been collected in North America, *Ptychodium plicatum* forms very large and highly branched, remarkably lustrous mats on boulders in alpine areas. In addition, leaves of *P. plicatum* are much larger and excessively plicate throughout, laminal cells are linear, and basal cells are distinctly thick-walled and pitted. Paraphyllia are also multiform. However, they are not prorate and only somewhat branched.

Variation: Most of the variation in *Lescuraea radicosa* var. *denudata* is in leaf length and width, being 1.42-2.38 mm long x 0.52-1.01 mm wide (usually 1.65-2.24 mm long x 0.72-0.92 mm wide), with leaf and laminal cell shape mostly homogeneous. Rhizoids and branches are generally few or lacking, but may be more numerous in the alpine-subalpine transition zone. Cell length tends to be homogeneous within, but often variable between specimens. Paraphyllia are always numerous, with the filamentous paraphyllia distinctly prorate and branched.

Habitat: *Lescuraea radicosa* var. *denudata* occurs predominantly on soil beneath *Cassiope* sp., various grasses, and other herbs in alpine meadows and tundra, often near late snowpatches. This taxon sometimes grows on somewhat sheltered rocks and bouders in areas of high elevation. Elevation: approximately 976-2500 metres (mostly 1700-2400 m, rarely less than 1600 m).

Distribution: *Lescuraea radicosa* var. *denudata* is common in North America and has been collected from southwestern and southeastern British Columbia, including Vancouver Island; Jasper National Park, Wilmore Wilderness Area, and southern Alberta; the Alexander Archipelago and the Aleutian Islands in Alaska; and Washington. Single collections were made in Montana and in Wyoming. *Lescuraea radicosa* var. *denudata* is also known from Greenland, Iceland, Sweden, and from the Alps.

Specimens examined: EUROPE: AUSTRIA: Salzburg: in Lungau – *Breidler* 24. Juli 1885 (BP – lectotype of Ptychodium oligocladon), Mittersill – *Breidler* August 1879 (BP – syntype of Ptychodium oligocladon), Pinzgau – *Breidler* 16. August 1879 (BP – syntype of Ptychodium oligocladon). **ICELAND:** Reykjavik – *Wallace & Crundwell 181* (UC/JEPS, CANM). **SWEDEN:** Jämtland: Storlien – *Heddelius* (FH). **NORTH AMERICA: CANADA: Alberta:** Banff National Park: Parker Ridge – *Krieger 1527, 1529, 1530*. Jasper National Park: *MacFadden 4068* (MO), Bald Hills – *Krieger & Belland 1549, 1550, 1551, 1552* (ALTA), Mt. Edith Cavell – *Krieger 1559, 1560, 1561, 1563, 1564, 1566, 1567* (ALTA), Whistler Mountain – *Krieger & Belland 1618, 1619, 1620, 1621, 1622, 1623, 1624*, Pyramid Mtn – *Krieger & Belland 1644, 1645, 1646, 1647, 1648, 1651, 1653, 1654* (ALTA). Kananaskis Country: Highwood Pass – *Krieger 1710* (ALTA). Little Elbow

River – *Bird 8758* (CANM). Wilmore Wilderness Area: E. of Hardscrabble Pass and S. of Cavass – *Krieger 1750, 1752, 1762* (ALTA), Hardscrabble Pass – *Krieger 1784* (ALTA). **British Columbia:** near Kamloops: Pass Lake – *Brinkman 335* (MO). Glacier District: Nakimu Caves – *MacFadden 17981* (MO). Sandon: Jackson Basin – *MacFadden 406* (MO). Selkirk Mts: Asulcan Creek – *Macoun 374* (S – lectotype of Pseudoleskea sciuriodes var. denudata, isotypes – S, F, MICH, MO, NY, UC/JEPS, US). Wilmer: Paradise Mine – *MacFadden 8792* (MO), *MacFadden* (NY – as Baur Musci Eur. et Amer. Exsiccati no. 2182). Mt. Liumchen: Church Mtn Area – *Schofield 63165* (UBC). W. side of Tkope River – *Schofield & Godfrey 97881* (UBC). Yaho Valley – *MacFadden* (MO). Vancouver Island: Strathcona Provincial Park: Buttle Lake – *Spence & Glass 1545* (UBC), E. side Buttle Lake – *Krieger & Hebben 1857* (ALTA). **GREENLAND:** Qasigialik Fjord – *Holmen 63-702* (NY). **USA: Alaska:** Aleutian Islands: Adak Island – *Jordal & Miller 3258* (CANM). Alexander Archipelago: Glacier Bay – *Boas, Lawrence, Reiners & Taylor 10341* (UBC). **Montana:** Columbia Falls – *Williams 343* (MO). **Washington:** Cascade Mts: Goat Mts – *Allen 154* (MO). Olympic National Park – *Spence 1262* (UBC). **Wyoming:** Beartooth Mts – *Welch 16578* (CANM).

Lescuraea saviana (DeNot.) E. Lawton, Bull. Torr. Bot. Cl. 84: 295. 1957. Figures 2.47-2.49

Leskea saviana DeNot., Musc. Ital. Spic. 8. 1837.

Type: "Ex appennino Etrusco Cl. PETRUS SAVI misit." [*Savi 821*] (annotation: as *Leskia saviana*) **Holotype – RO !**

Pseudoleskea atrovirens var. *acutifolia* Velen., Oesterr. Bot. Zeitschr. 52: 121. *Fide* Wijk *et al.* 1967. **Type:** "An Baumstämmen bei Bela Cerkva (Stř.)." [Bulgaria] **Holotype –** (not seen)

Pseudoleskea illyrica Glow., Verh. Zool. Bot. Ges. Wien 57: 227. 1907.

Type: "Plaša planina, ca. 1300-1600 m., auf Stämmen alter Rotbuchen." "Sie scheint an geeigneten Orten der dinarischen Alpen …, Vom Verfasser auch auf dem später zu erwähenden Orijen-Berge und bereits im Jahre 1896 an einigen Orten in Montenegro beobachtet wurde." [Herzegovina and Montenegro; *Glowacki*] **Lectotype GJO !** (*Glowacki*

25181 / 17928, lectotypus)**; syntypes – GJO !** (12 specimens)

Pseudoleskea radicosa var. *meridionalis* Culm. *in* Amann, Flore des Mousses de la Suisse 2: 285. 1912. *Fide* Wijk *et al.* 1967. **Type:** "Le n° 83 du Bryotheca Europ. Meridionalis de Fleischer et Warnstorf…." **Holotype** – (unavailable)

Lescuraea atrovirens var. *saviana* (DeNot.) Mönk., Die Laubm. Eur. 693. 1927.

Pseudoleskea saviana (DeNot.) Latz., Beih. Bot. Centralblatt 48(2): 499.1931.

Pseudoleskea radicosa subsp. *saviana* (DeNot.) Giac., Annali Bot. 23: 7. 1946.

Pseudoleskea radicosa var. *illyrica* (Glow.) Giac., Annali Bot. 23: 7. 1946.

Pseudoleskea atrovirens var. *illyrica* (Glow.) Giac., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser 5, 4: 256. 1947.

Pseudoleskea incurvata var. *meridionalis* (Culm.) Podp., Consp. 531. 1954.

Nomenclatural notes: *Leskea saviana* was described by De Notaris in 1837 from a specimen collected by Savi. The holotype at RO was diffult to obtain. Fortunately, it was made available for a short-term loan. Packet information reads "*Leskia polyantha*, In appennino etruriae, *Savi 821*," handwritten by Savi. DeNotaris (1837) described *Leskea saviana* from this material and published it under the name *Leskia saviana.* Lawton (1957) indicated that an isotype exists in Mitten's herbarium at NY. Unfortunately, no specimens were seen.

Velenovský described and published *Pseudoleskea atrovirens* var. *acutifolia* from specimens collected on trees at Bela Cerkva (Stř.), in Bulgaria. Although no specimens were reviewed in this revision, Wijk *et al.* (1967) consider *Pseudoleskea atrovirens* var. *acutifolia* synonymous with *Pseudoleskea saviana* (DeNot.) Latz. (= *Lescuraea saviana*).

Pseudoleskea illyrica was described by Glowacki in 1907 from specimens collected (by himself) in the 'Occupation zones' of Europe. Although Glowacki does not give a clear type citation, lacking a type designation including a collection number and date, information gleaned from his protologue indicates that Glowacki collected specimens on old *Fagus* sp. trees on Plaša planina, Herzegovina between 1300 and 1600 metres. Glowacki (1907) revealed that this species seems to be more widespread in the

Dinaric Alps, having also collected it from the 'Orijen-Berge' in Herzegovina and from Montenegro in 1896. Presently, it is still unknown when Glowacki collected the specimens from Plaša planina, since no date is given. Type material of *Pseudoleskea illyrica* specifically from Plaša planina is unavailable from all of the possible herbaria (GJO, JE, or KL) housing Glowacki's specimens. However, syntypes from the Orijen Mountains and from Montenegro dated from 1904 and 1896, respectively in GJO are clearly synonymous with *Lescuraea saviana.* A specimen collected by Glowacki in Montenegro (Lijeva rijeka am Fusse der … 950 m. 11.08.1896, leg. J. Glowacki Inv.-Nr. 25181/17928) was chosen as the lectotype from among the syntypes due to the excellent plant habit and abundance of intact sporophytes.

Exsiccatae of Baumgartner, June 1911, issued by Bauer, Musci Eur. 1226 in CANM, and Baumgartner *2295* (as *Pseudoleskea illyrica*) in F, MO, UC/JEPS, and US, collected from the trunks of *Fagus* sp. on 'Orjen-Sattel'in Herzegovina, between 1300 and 1400 metres, were reviewed. Packet information reads 'locus classicus!' indicating Baumgartner collected these specimens from the same locality as those of Glowacki. The CANM and US specimens of Baumgartner have numerous sporophytes, and all specimens from the herbaria listed above, are clearly synonymous with *Lescuraea saviana.* Wijk *et al.* (1967) and Redfearn Jr. (1986) also place *Pseudoleskea illyrica* in synonymy with *Pseudoleskea saviana.*

Description: Plants small to medium-sized, somewhat soft and lax, forming loose to densely intertwining mats; yellow-green to green, older stems and branches somewhat brown; satin-glossy to ± dull. Stems prostrate, apices distinctly hooked; thin; elliptic when dry, somewhat round when moist; not or somewhat fragile when dry; outer cortical cells of 2-3 layers, orange, thick-walled; cells of medulla gradually large-lumened, hyaline; central strand distinct. Branching irregularly; branches short and numerous. Rhizoids smooth; red-brown; occasional; forming somewhat branched tufts along stems; matted tuft common near stem apex; few along branches. Paraphyllia multiform, small filamentous to foliose, unbranched; cells ± thick or thin-walled, quadrate to elongate; numerous on stems and branches. Stem leaves densely arranged; erect to somewhat appressed when dry, spreading when moist, the acumen erect to spreading somewhat;

distinctly concave below; asymmetric; somewhat to distinctly falcate; distinctly plicate; narrowly long decurrent; lanceolate, abruptly long acuminate, acumen as long or longer than leaf proper; 0.88-1.86 mm long x 0.38-0.78 mm wide, mostly 0.94-1.60 mm long x 0.44-0.65 mm wide. Margins distinctly serrate at apex, acumen distinctly serrate; broadly recurved from middle to lower acumen, somewhat recurved from lower acumen to base of leaf. Branch leaves similar in shape to stem leaves, somewhat smaller, distinctly serrate along acumen. Costa yellowish to orange-tinged; ending before apex to somewhat percurrent; stout below, remaining somewhat stout above, narrowing slightly in acumen; abaxial surface distinctly keeled; distinctly prorate along upper abaxial portion. Alar region large, extending nearly ½ up along margin to lower acumen; cells thin- to somewhat thick-walled, quadrate with slightly transverse-elongate cells interspersed; 4.8-12.0 µm long x 7.2-16.8 µm wide, mostly 7.2-12.0 µm long x 9.6-12.0 µm wide (rarely to 17.5 µm long). Basal cells thick-walled, rectangular to oblong-elongate; 7.2-28.8 µm long x 4.8-12.0 µm wide, mostly 12.0-19.2 µm long x 7.2-9.6 µm wide (rarely 21.6-28.8 µm long). Median cells somewhat thick-walled, oblong-fusiform to fusiform-linear, somewhat sinuose or rarely vermicular, sometimes rhomboidal or linear cells interspersed, ± homogeneous from costa to mid-leaf, cells of margin considerably smaller due to extension of alar cells; 7.2-36 µm long x 3.6-7.2 µm wide, mostly 12.5-22.5 µm long x 4.8-6.0 µm wide (rarely 25.0-37.5 µm long). Distal cells somewhat thick-walled, rhomboidal to oblong, sometimes oblong-fusiform; 7.2-24.0 µm long x 4.8-9.6 µm wide, mostly 12.5-17.5 µm long x 6.0-7.2 µm wide (rarely 20.0-25.0 µm long). Papillae round; distinctly prorate; lower and median cells slightly prorate, distal cells distinctly prorate; stem and branch leaves equally prorate; prorae common on abaxial and adaxial leaf surfaces. Perichaetia rare, satin and translucent; perichaetial leaves erect, linear-lanceolate, abruptly acuminate to a long slender point, somewhat serrate above, clasping seta throughout; costa stout, percurrent; basal cells lax, fusiform-rectangular, distal and median cells fusiform-linear, slightly prorate at both ends. Perigonia occasional, limited to few along stems, perigonial bracts ovate, short ligulate-acuminate, appressed, concave and entire; costa ending in acumen; basal cells lax, fusiform-oblong, distal and median cells somewhat thick-walled, fusiform-linear, papillae lacking. Sporophyte occasional. Seta smooth; orange to red-brown; dextrorse below,

± distinctly sinistrorse above; 6.0-9.0 mm long. Capsule erect, cylindric, and symmetric to somewhat inclined; orange to red-brown; somewhat rough and dull; somewhat constricted below mouth when dry, mouth ± flaring outward, swollen when moist; 1.0-1.5 mm long. Operculum short-rostrate. Peristome inserted along mouth of capsule. Exostome segments orange-brown below, yellow-hyaline above; lanceolate, gradually acuminate, somewhat 'shouldered'; strongly incurved, distal portions touching endostome segments; joined at base to form an orange-brown band; proximal dorsal surface with horizontal ridges along basal plates, fine horizontal striations from ⅓ to nearly ½ height of tooth, fine papillose-striae in oblique or circular pattern in median portion, distal portion rounded papillose; apex somewhat blunt; ventral surface highly trabeculate; 265-382 µm long. Endostome segments yellowish-brown to brown; as long or somewhat shorter than exostome; linear-lanceolate, gradually acuminate, distinctly keeled, straight; narrowly to distinctly perforate along median line; narrowly spaced; joined to form a median basal membrane of similar colour ¼ the height of segments; dorsal and ventral segment surfaces sparse and minutely papillose throughout; 216-382 µm long; cilia lacking or sometimes vestigial protuberances visible. Spores minutely papillose; 12.0-16.8 µm in diameter, mostly 14.4-16.8 µm (rarely less than 12.0 µm in diameter). N = not reported.

Diagnostic characters: *Lescuraea saviana* has broadly recurved leaf margins resulting in an abrupt and long acumen. The long and broadly recurved acumen, as well as the distinctly prorate lower median to distal leaf cells are characteristic for this taxon. The somewhat thick-walled and slightly vermicular, fusiform-linear median cells are striking. The capsule is erect or rarely slightly inclined, and the peristome is rather reduced. The endostome segments are narrowly keeled to distinctly terete, and the basal membrane is low and cilia are lacking. Vesigial protuberances are rarely visible. This taxon occurs predominantly on bark of shrubs and on trees.

Lescuraea saviana has been confused with both *L. radicosa* and *L. incurvata* due to its intermediate characters, although laminal cells of *L. radicosa* are never thick-walled, nor distinctly prorate. If *L. radicosa* has prorate leaf cells, then they are quite indistinct and restricted to the distal cells. *Lescuraea incurvata* on the other hand, has very thick-walled, short and irregular cells that are highly prorate. The differences between *L. saviana* and the other two taxa are in the size, shape, thickness, and papillosity of the laminal cells, as well as in a more reduced peristome.

Variation: Leaf length and width varies from 0.88-1.86 mm long x 0.38-0.78 mm wide (usually 0.94-1.60 mm long x 0.44-0.65 mm wide), both within and between specimens. Some stem leaves are less conspicuously long acuminate due to less broadly revolute margins.

Habitat: *Lescuraea saviana* occurs on bases of trees and on decayed wood on soil. It is also found on granite and quartzite boulders in forests and on rock outcrops, occasionally near streams or other water sources. Elevation: approximately 1000-2500 metres (occasionally less than 1000 m).

Distribution: *Lescuraea saviana* is rare in North America. It has been collected from a few of the Aleutian Islands; Washington; Idaho, and the northern portion of California. A single specimen from British Columbia, *Tan & Ensing 77-1786* (US) is *L. atricha*. *Lescuraea saviana* is common in central and southern Europe, and is found predominantly on bark at bases of *Fagus sylvatica*.

Specimens examined: Europe: Bulgaria: (ALA). **Georgia:** Caucusus Mtns: Sukhumi – *Vašák* (COLO). **Greece:** Mt. Olympus – *Baumgartner 295* (US). **Montenegro:** Orjen-Berge – *Glowacki 25181/17925, 25181/18196* (GJO), Orjen-Sattel – *Baumgartner 1226* (CANM), *Baumgartner 2295* (MO, F, UC/JEPS, US). Montenegro – *Glowacki 25181 /17928* (GJO – lectotype of Pseudoleskea illyrica), *Glowacki 21058, 21060, 21062, 25181/17926, 25181/17927, 25181/17929, 25181/17930, 25181/17931, 25181/17932* (GJO – syntypes of P. illyrica). **Hungary:** Carpathian Mountains: Tatra Mountains: Kékes Mountain near Parád – *Boros Cryptogamae exsiccatae 3993* (COLO). **Italy:** *Savi 821* (RO – holotype of Leskea saviana), *Amano* anno 1838 (RO), *Orsini* anno 1837 (RO), *Lunardi 245* (WTU). **Poland:** Tatry granitowe – *Zmuda 137* (CANM). **Slovakia:** *Boros 4691* (COLO). **Slovakia/Czech Republic:** (as Czechoslovakia) Krain, Schneeberg bei Laar – *Glowacki* 7.12.1910 (JE). **Turkey:** Ilica – *Stanton &*

Henderson 6310 (DUKE). **NORTH AMERICA: USA: California:** Siskiyou Co. – *Norris 11891* (UC/JEPS). **Idaho:** Valley Co.: – *Hermann 20281* (DUKE), Summit Co. – *unknown collector* (MO). **Washington:** Clallam Co. – *Lawton 2597* (WTU), Pierce Co.: foot of Emons Glacier – *Frye* (WTU), Snohomish Co. – *Douglas 642* (ALTA).

Lescuraea stenophylla (Ren. & Card.) Kindb., Eur.& N.Am. Bryin. 1:26. 1896. Figures 2.50-2.52

Pseudoleskea stenophylla Ren. & Card. *in* Röll, Botanisches Centralblatt 44: 21. 1890. **Type**: "Cascades: Washington, Easton, Kitchelos Lake" [*Dr. Julius Röll*, 16. June 1888; under the auspices of Dr. Dieck of the National-Arboretums in Zöschen by Merseburg] **Holotype – BM !**

Hypnum radicosum var. *gracilis* Lesq. & James., Man. N.Am. Mosses 320. 1884. *Fide* Wijk *et al.* 1964. **Type**: "HAB. Banks of the Portage River, British America, on roots of trees near the ground and the variety in dryer situations, on branches of trees (*Drummond* n. 225)." **Holotype –** (not seen)

Lescuraea imperfecta C. Müll. & Kindb. *in* Macoun, Cat. Can. Plants Part VI, Musci: 170. 1892. **Type**: "On both earth and bark at the bases of trees on both sides of the Columbia River at Revelstoke, British Columbia, May 19th, 1890. (*Macoun*)." [Canadian Musci No. 489.] **Holotype – S** (not seen)**; isotypes – COLO !, FH !** (3 specimens)

Pseudoleskea congesta var. *gracilis* (Lesq. & James.) Par., Ind. Bryol. ed. 2, 4: 104. 1905.

Lescuraea rigescens Arn. & C. Jens., Naturw. Unt. Sarekgeb 3: 212. 1910. *Fide* Wijk *et al.* 1964. **Type:** protologue unavailable

Pseudoleskea atrovirens subsp. *stenophylla* (Ren. & Card.) Giacom., Atti Ist. Bot. Univ. Lab. Critt. Pavia ser. 5, 4: 256. 1947.

Nomenclatural notes: The holotype of *Pseudoleskea stenophylla*, described by Renauld & Cardot, is at BM. The protologue indicates that Dr. Julius Röll, under the auspices of Dr. Dieck of the National-Arboretum in Zöschen by Merseburg, collected specimens from North America in 1888, to be returned and used to teach botanists about foreign mosses. The BM specimen clearly supports the information given in the protologue and in the type citation. Not included in the protologue are collection numbers of '672. 673' on the packet label. Lawton (1957) indicated that the holotype of *P. stenophylla* is "probably at PC," and cites an isotype as *Roell 672* at NY. No specimens were reviewed from PC, and no isotype from NY was found.

Lesquereux and James (1884) described *Hypnum radicosum* var. *gracilis* from specimens in Drummond's first collection (no. 225). Wilson was the first to realise that Drummond's collection no. 225 (as *Hypnum tenax*) was actually a mixed collection; the two elements are known today as *Lescuraea stenophylla* and *Lescuraea radicosa*. No specimens have been studied from the herbaria of Lesquereux and James.

Müller and Kindberg described *Lescuraea imperfecta* in Macoun's 1892 'Catalogue of Canadian Plants', under 'Canadian Musci No. 489'. No specimens have been seen from S. However, material from both COLO and FH have been studied and are cited as isotypes. There are some slight disparities between the packet information from the isotypes listed and that of the type citation. The citation indicates that the type was collected "on both earth and bark at the bases of trees on both sides of the Columbia River at Revelstoke, B.C., May 19th, 1890." However, packet labels from COLO and FH indicate that specimens were collected from rotten trunks and small trees in woods, from the west side of the Columbia river at Revelstoke, B.C., May 9th, 1890. Although the substrate and collection date are somewhat different from those of the type citation, they are all specimens of Müller and Kindberg, recognised as 'n. sp., Canadian Musci No. 489'. Upon investigation of the three specimens in FH, it became clear that some had been collected from mineral soil and others from bark, as mineral soil and bark remnants were evident. This information supports the view that the COLO and FH specimens are isotypes. Lawton (1957) indicated that type material of *L. imperfecta* (as *Macoun* Can. Musci 489) is found at S-PA, CANM, and WTU. Unfortunately, no specimens were seen from any of these herbaria.

Arnell and Jensen described *Lescuraea rigescens* in 1910. Unfortunately, the protologue was unavailable and as such, type material was not reviewed. Wijk *et al.* (1964) consider *Lescuraea rigescens* a synonym of *Lescuraea stenophylla.*

Description: Plants very small to small-sized, soft, and lax, forming densely intertwining mats; yellow-green to green, with older stems and branches somewhat brown; somewhat satin-glossy. Stems prostrate, thin, apices somewhat to indistinctly hooked; somewhat to distinctly round when dry or moist; fragile when dry; outer cortical cells of 1-2 layers, orange-red, thick-walled; cells of medulla thin-walled, rounded, abruptly large-lumened, hyaline; central strand distinct. Branching irregularly, branches short and numerous, 2° branches few to numerous, usually short and prostrate. Rhizoids smooth; red-brown; common or occasional; branching slightly; forming tufts along stem; matted tufts common near stem apex; few along branches. Paraphyllia multiform, filamentous to foliose, unbranched; cells thin-walled, rhomboidal to elongate; numerous on younger portions of stems and branches. Stem leaves densely to ± sparsely arranged; erect-patent to slightly appressed when dry, spreading slightly when moist; acumen long and slightly flexuose and spreading; straight, rarely somewhat concave below; symmetric; indistinctly plicate; narrowly long decurrent; lanceolate and gradually long acuminate; acumen distinctly longer or as long as the leaf proper; 0.93-1.96 mm long x 0.30-0.57 mm wide, mostly 1.15-1.35 mm long x 0.33-0.45 mm wide. Branch leaves similar in shape to stem leaves, somewhat smaller, usually serrulate at apex. Margins somewhat serrate at apex, acumen mainly entire; narrowly recurved from lower acumen to leaf base. Costa yellowish-green; distinctly percurrent; somewhat stout below, narrowing mid-leaf and into lower acumen; abaxial surface indistinctly keeled; somewhat prorate along upper abaxial portion. Laminal cells ± distinctly echlorophyllose, somewhat translucent. Alar region small, extending up to ¼ up leaf margin; cells thin-walled, somewhat lax; quadrate to oblong; 9.6-16.8 μm long x 7.2-12.0 μm wide, mostly 12.0 μm long x 9.6 μm wide. Basal cells thin-walled, somewhat lax; short-rectangular to oblong; 12.5-28.0 μm long x 4.8-12.0 μm wide, mostly 17.5-25.0 μm long x 8.4-9.6 μm wide (rarely to 35.0 μm long). Median cells thin-walled; oblong-rhomboidal near costa, fusiform-rhomboidal in centre, becoming rectangular-oblong near leaf margin; 15.0-38.0 μm long x 4.8-10.8 μm wide, mostly 17.5-25.0 μm long x 6.0-10.0 μm wide (rarely to 38.0 μm long). Distal cells thin-walled; irregularly rhomboidal to fusiform-oblong; 10.0-25.0 μm long x 6.0-12.0 μm wide, mostly 15.0-17.5 μm long x 7.2- 9.6 μm wide (rarely to 30.0 μm long). Papillae round; on upper cell lumen, rarely somewhat prorate; median and distal cells somewhat papillose; branch leaves more distinctly papillose; papillae common on abaxial and adaxial leaf surfaces. Perichaetia common, satin and translucent; perichaetial leaves erect, lanceolate, gradually long-acuminate, somewhat serrate above; clasping seta throughout; costa ± weak, narrow, extending into lower acumen; basal cells lax, fusiform-rectangular, distal and median cells thin-walled, fusiform-linear, papillae lacking. Perigonia common, numerous along stems, sometimes several on branches; perigonial bracts ovate, abruptly acuminate, appressed, concave and entire; costa lacking; basal cells lax, fusiform, distal and median cells thin-walled, fusiform; papillae lacking. Sporophyte common. Seta smooth; yellow-orange to orange-brown; distinctly dextrorse below, somewhat to distinctly sinistrorse above; 6.0-9.0 mm long (rarely from 14.0-25.0 mm long). Capsule erect, short cylindric, and symmetric; somewhat rough and dull; slightly constricted below mouth when dry, mouth flaring outward somewhat, swollen when moist; 1.0-3.0 mm long (rarely less than 1.0 or greater than 4.0 mm long). Operculum conic. Peristome inserted along mouth of capsule, greatly reduced. Exostome teeth orange-brown below, yellow-hyaline above; lanceolate, gradually acuminate, somewhat 'shouldered'; often recurved below and incurved above, revealing entire endostome; joined at base to form a dark red-brown band; proximal dorsal surface with horizontal ridges to ⅓ height of tooth, sometimes finely papillose-striate or striate in part, fine papillose striae or papillae in oblique or circular pattern in median portion, sparse and rouned-papillose in distal portion of tooth; apex somewhat blunt; ventral surface distinctly trabeculate; 275-345 μm long. Endostome segments orange-red to red-brown; as long or shorter than exostome; linear, terete, typically without a keel, slightly inflexed; narrowly to widely perforate along median line; widely spaced, joined to form a low basal membrane of similar colour ¼ height of segments; dorsal and ventral surfaces somewhat dense and coarsely papillose throughout; 187-237 μm long; cilia lacking, occasional vestigial protuberances visible between segments. Spores coarsely papillose, 16.8-19.2 μm in diameter. N = 8 (Fritsch 1982).

Diagnostic characters: *Lescuraea stenophylla* forms small, lax, and soft-looking prostrate mats on small branches of shrubs, often near sources of water. Stem and branch leaves are lanceolate, with a long narrow acumen. A single round papilla, evident on the upper cell lumen of most distal and some median cells, will distinguish this taxon from smaller forms of *L. radicosa* var. *radicosa*. The proliferation of perigonia on male plants, often with >10 on a single stem, is also an identifying feature of this taxon. The erect and short cylindric capsules with exostome teeth recurved and then incurved again, revealing the entire endostome, is typical for this taxon and has not been seen in other taxa within *Lescuraea*. The distinctly orange to red-brown endostome features narrow and terete segments that are gently inflexed, as well as a low basal membrane. This peristome is also common in taxa of *Leskea*. However, capsules in these taxa are all very long and narrowly cylindric. Gametophytically, *Lescuraea stenophylla* cannot be confused with *Leskea*, since taxa in the latter genus have ovate leaves that are gradually acute or even blunt, as well as having round or isodiametric cells with a single minute papilla over the central lumen. On the other hand, *Lescuraea radicosa* var. *radicosa* is often small and lax, and appears similar gametophytically to *L. stenophylla*. However, the latter is differentiated by its peristome, type of papillae, and by its habitat. Where a rounded papilla is situated over the upper region of the cell lumen in *L. stenophylla*, papillae are nearly lacking or cells are somewhat prorate in *L. radicosa*. The peristome of *L. radicosa* is not as reduced, the exostome is incurved with the teeth vanishing between the segments, and the endostome is yellowish-hyaline and distinctly keeled. *Rigodiadelphus baileyi* also has papillae similar to *L. stenophylla*. However, *R. baileyi* can be differentiated by: a large and robust habit on branches of shrubs; stem transverse section with numerous rows of outer cortical cells, and lack of a central strand; leaves with a long hyaline point; highly pitted laminal cells; smooth globose-cylindric capsule; and by its unreduced peristome. See the discussion on *R. baileyi* for diagnostic characters.

Variation: Leaf length and width varies from 0.93-1.96 mm long x 0.30-0.57 mm wide, (usually 1.15-1.35 mm long x 0.33-0.45 mm wide) both within and between specimens. In shorter leaves, the acumen is as long or sometimes somewhat shorter than the leaf proper. Frequency of papillae also varies both within and between specimens, with some stem leaves appearing to have no papillae, while others have many. Capsule size varies greatly even within specimens, with small and medium urns arising from a single plant.

The endostome segments are rarely yellowish-hyaline. This coloration is found in more exposed specimens.

Habitat: *Lescuraea stenophylla* occurs on bark of lower branches, as well as on the bases of *Alnus* and *Salix* species at the edges of montane to subalpine forests, often near creeks or other sources of water. It is also common on other shrubs or on bark at bases of *Acer* species. It is rarely found on boulders, soil, or on limestone rock. Elevation: approximately 549-2074 metres.

Distribution: *Lescuraea stenophylla* has been collected from: the Aleutian Islands and the Alexander archipelago of Alaska; extensively in southern British Columbia, including Queen Charlotte and Vancouver Islands; the Rocky Mountains of both British Columbia and Alberta; the northwestern portions of Montana and Wyoming; northern Idaho, Utah, and California; and western portions of both Oregon and Washington state. It is disjunct in eastern North America in the Gaspé, Quebec; Cape Breton, Nova Scotia; and Gros Morne, Newfoundland. This species is reported from Europe, although rare. No collections from Europe were examined.

Specimens examined: NORTH AMERICA: CANADA: Alberta: Banff National Park: Lake Agnes – *Krieger & Hebben 1887* (ALTA). Coleman – *Bird & Lakusta 18239* (CANM). Jasper National Park: Mt. Edith Cavell – *Krieger 1558, 1568, 1576, 1578* (ALTA). Waterton Lakes National Park: *Hermann 20572* (CANM, UBC); Cameron Lake – *Krieger & Hebben 1801, 1803* (ALTA); Crandell lake – *Krieger & Hebben 1825*. **British Columbia:** Popkum: Bridal Veil Falls – *Schofield 43651* (CANM). Bugaboo Glacier Provincial Park: Big Fish Lake – *Tan & Ensing 77-1739* (UBC). Buntzen Lake – *Schofield & Taylor 106424* (UBC). N. Cascade Mts: Cluster Ridge -- *Schofield 57417* (CANM). near Cheekeye: Squamish River – *Schofield 20143* (CANM). Clearwater: Bear Creek Falls – *Boas* (CANM). Fraser Canyon: Alexander Bridge – *Schofield 71577* (CANM). Garibaldi – *Schofield 26085* (CANM). Gerrard: Trout Lake – *Bell* (UBC). S. of Hope: Maselpanik Creek – *Boas 84* (CANM). Howe's Sound: Nelson Creek – *Schofield 67736* (CANM). Headwater of Nicknaqueet River – *Schofield 85895* (CANM). Mt. Robson Provincial Park – *Franko 80-83* (UBC). North Vancouver: Mount Seymour –

Krieger & Hebben 1841, 1842, 1846, 1850 (ALTA), *Schofield 14559* (UC/JEPS), *Schofield 78727* (CANM). Pemberton: Nain Falls – *Schofield & Belland* 92805 (CANM). Queen Charlotte Islands: Moresby Island – *Persson* (OSC/ORE). Selkirk Mtns: Kokanee Glacier Provincial Park – *Tan & Ensing 77-685* (CANM); Revelstoke – *collector unidentified* (COLO); Roger's Pass – *Macoun* May 9th, 1890 (isotypes of Lescuraea imperfecta – COLO, FH (3 specimens)). Sasquatch Lake: Slocan – *Tan & Ensing 77-730* (UBC). Selwyn range – *Vitt 34124* (COLO). near Squamish – *Schofield 20605* (CANM). Vancouver Island: Tofino: Taylor River Flats – *Schofield 13552* (CANM). Kittitas Co. – *Ireland 8150* (CANM). Wells Gray Provincial Park – *Foreman & Krajina 70-131* (UBC). **Newfoundland:** Gros Morne Provincial Park – *Belland & Schofield 11250* (CANM). **Nova Scotia:** Cape Breton: Victoria county – *Schofield & Belland 88386* (CANM). **Quebec:** Florillon National Park – *Belland 14958* (CANM). **USA: Alaska:** Aleutian Islands: Aniakchak National Monument – *Hasselbach* (ALA). Attu Island – *Talbot & Talbot 88-796* (UBC). Izembek National Wildlife Reserve – *Schofield 99473, 99751, 100284* (ALA). Kenai Peninsula: Chisik Island – *Schofield & Talbot 98719* (UBC), *Talbot 87-11-5* (UBC). Kodiak Island – *Sharp 90* (UBC). Simeonoff Island – *Schofield & Talbot 104116* (UBC). Central Pacific Coast District – *Viereck & Viereck 2079* (ALA). Queen Inlet -- *Worley & Rawson 13179* (UBC). Alexander Archipelago: Glacier Bay: Gilbert Island – *Worley & Boas 10783* (UBC), Sebree Island – *Worley et al. 10441* (UBC), Nunatak to Goose cove – *Worley 10566* (UBC); Mitkov Island – *Worley & Schofield 8486* (UBC). **California:** Del Norte Co. – *Norris 47909* (UC/JEPS), *Norris 67796* (OSC). Humboldt Co. – *Norris 47812* (UC/JEPS). Siskiyou Co. – *Spjut 9980* (UC/JEPS). **Idaho:** Bonner Co. – *Anderson 22552* (FH). Idaho Co. – *Wagner 776* (OSC/ORE). Kootenai Co. – *Leiberg 320* (CANM). **Montana:** Flathead Co. – *Stickney 2015* (CANM). Glacier Co. – *Hermann 20461* (DUKE). Lake Co. – *McCune 2931, 3828, 5420* (OSC). Lincoln Co. – *Schofield 12000* (UBC). Stanta Lake: Newberry's Ranch – *Williams 255* (ALA, CANM, UBC). **Oregon** – Clackamas Co. – *Pechanec 1277* (UBC). Clatsop Co. – *Schofield & Godfrey 67905* (UBC), *Schofield & Christy 81850* (UBC). Deschute Co. – *Schofield & Lyford 60187* (UBC). Hood River – *Holmberg 2043* (OSC). Lane Co. – *Schofield & Lyford 60172* (UBC). Linn Co. – *Jonsson 374 B/94* (OSC). Multnomah Co. – *Ireland 7152* (CANM). **Utah:** Summit Co. – *Flowers 7378* (ALA).

Washington: Cascades: Easton: Kitchelos Lake – *Röll* (BM – Holotype of Pseudoleskea stenophylla). Chelan Co. – *Ireland 8102* (CANM). Clallam Co. – *Ireland 6593* (WTU). Jefferson Co. – *Becking 5309 P1046* (WTU). King Co. – *Lawton 5618* (WTU). Kittitas Co. – *Ireland 8150* (CANM). Lewis Co. – *Ireland 8041* (CANM). Mason Co. – *Lawton 3265* (WTU). Mount Olympic National Park – *Harthill 3685* (COLO). Mt. Rainier National Park – *Foster* (COLO). Pierce Co. – *Harpel 12796* (WTU). Skamania Co. – *Becking 5308232* (WTU). Snohomish Co. – *Lawton 2600* (WTU). Whatcom Co. – *Becking 530550* (WTU). **Wyoming:** Grand Teton National Park – *Flowers 3833* (COLO).

2.6 *Rigodiadelphus* in North America

Rigodiadelphus Dixon, J. Bot. Brit. For. 74: 3. f.3. 1936.

Type: *Rigodiadelphus octoblepharis* Dixon (type not seen)

Lesquereuxia subg. *Adelphodon* Lindb., Contr. Flor. Crypt. Asiae-Boreali-Orient. 245. 1872. **Type:** *Lesquereuxia robusta* Lindb. **Holotype – H-SOL !**

Lescuraea subg. *Adelphodon* (Lindb.) Broth., Die Nat. Pflanzenf. I(3): 998. 1907.

Lescuraea Lindb. *ex* Broth., Nat. Pflanzenf. 2. Aufl. 11: 475. 1925., *homo. illeg.*

Type: *Lescuraea robusta* (Lindb.) Lindb. *ex* Broth.

Lescuraea subg. *Tricholeskea* E. Lawton, Bull. Torr. Bot. Cl. 84(5): 342. 1957. ***synon. nov.*** **Type:** *Lescuraea baileyi* (Best & Grout *in* Grout) E. Lawton

Neolescuraea Noguchi, Jour. Hatt. Bot. Lab. 36: 521. 1972.

Type: *Neolescuraea robusta* (Lindb.) Noguchi

Nomenclatural notes: Currently, the genus *Rigodiadelphus* Dixon consists of one North American, *R. baileyi* (Best & Grout *in* Grout) comb. nov., and two Asian species, *R. robustus* (Lindb.) Noguchi and *R. arcuata* Noguchi. Subgenus *Adelphodon* devised by Lindberg in 1872 was to accomodate the single Japanese taxon *Lesquereuxia robusta*. However, *Lesquereuxia* had been published by Boissier (1853) as a new genus in the Scrophulariaceae (Rohrer 1986). Lindberg's later described generic name *Lesquereuxia* was meant as a revised spelling of *Lescuraea*, and therefore it was invalid. Fleischer (1923) confused the issue by recognising both *Lescuraea* and *Lesquereuxia*. As discussed previously, Fleischer (1923) believed that species of subgenus *Adelphodon* were phylogenetically unrelated to the rest of the genus *Lescuraea*. Lawton (1957) also recognised this difference. In her revision of *Lescuraea* in Europe and North America, Lawton (1957) established that gametophytically, *Lescuraea baileyi* (Best & Grout *in* Grout) E. Lawton "is not closely related to the other species in the genus, but rather resembles *Lesquereuxia robusta* from Japan." Although Lawton (1957) revealed gametophytic similarities between the two aforementioned species, she indicated that the "radically different peristome" of *Lesquereuxia robusta*, separates it from *Lescuraea baileyi* and other species in *Lescuraea*. Due to the gametophytic differences between *Lescuraea baileyi* (Best & Grout *in* Grout) E. Lawton and the rest of the species in *Lescuraea*, Lawton (1957) proposed subgenus *Tricholeskea* to accommodate this taxon.

In 1936, Dixon described and published the monotypic *Rigodiadelphus octoblepharis* from a specimen from Japan. Some time later, Noguchi (1972) proposed the name *Neolescuraea* in place of Lindberg's invalid name *Lesquereuxia*. He soon realised that he had synonymized *Neolescuraea robusta* and *Rigodiadelphus octoblepharis*. Since *Rigodiadelphus* is an earlier name, and Dixon's (1936) solitary species is synonymous with Lindberg's *Lesquereuxia robusta*, Noguchi (1972) made the new combination *Rigodiadelphus robustus* (Lindb.) Noguchi.

In the current revision of *Lescuraea* and *Pseudoleskea*, the striking gametophytic and partial sporophytic similarities between *Pseudoleskea baileyi* Best & Grout in Grout and *Rigodiadelphus robustus* have lead to the recognition of *Rigodiadelphus baileyi* as a new combination.

Description: Plants large-sized, robust; mostly olive-green; dull. Stems distinctly elliptic; outer cortical cells numerous, mostly 4-8; central strand lacking. Paraphyllia lacking. Stem leaves distinctly falcate-secund; lanceolate and gradually acuminate to a long, hyaline point. Costa dissipating in lower acumen; scarcely prorate along upper abaxial portion. Alar region large; cells mostly obliquely quadrate. Laminal cells thick-walled, distinctly pitted throughout, elongate to distinctly linear. Papillae round, on upper cell lumen, often appearing somewhat prorate. Dioicous. Perichaetia lustrous and opaque; perichaetial leaves spreading, broadly lanceolate, gradually acuminate; costa very weak and narrow, ending mid-leaf or below. Sporophyte rare. Capsule globose-cylindric, symmetric; red-purple, becoming orange when old; distinctly smooth and lustrous. Operculum conic, with a distinct minute nipple or apiculus. N = 8, 16 (Fritsch 1982).

Rigodiadelphus baileyi (Best & Grout *in* Grout) M. Krieger ***comb. nov.*** * Figure 2.53-2.55

Pseudoleskea baileyi Best & Grout *in* Grout, N.Am.Musc.Pl. 474. March, 1917.
Type: "On branches of shrubs near ground beside Sunset Trail, Cascade summit, Washington. Under 30 ft. of snow last winter, 1915-1916. J.W. Bailey no. 474, July 19, 1916. 3000 ft." **Lectotype – NY !** (lectotypus); **isotypes – DUKE !, F !, US !, MICH !, UC/JEPS !**

Lescuraea baileyi (Best & Grout *in* Grout) E. Lawton, Bull. Torr. Bot. Cl. 84: 342. 1957.

Nomenclatural notes: *Pseudoleskea baileyi* was described by Best and Grout (1917) from specimens collected by Bailey in Washington. There is only one specimen at NY in which the packet label matches the type citation, including the collection date and collection number. This specimen is designated as the lectotype. There is another specimen at NY, although lack of a collection number and a collection date of July 13, 1916, indicates that this is not type material. Packet labels of specimens from DUKE, F, US, MICH, and UC/ JEPS match the type citation exactly and are listed as isotypes.

Since the type collection is sterile and epiphytic on live branches, fruiting material collected by Bailey on rocks in 1924 from the same general locality were sent to the New York Botanical Garden for review. Shortly thereafter, Mrs. Britton wrote a letter to Williams suggesting he should describe and prepare a plate of the sporophyte of *Pseudoleskea baileyi*, and publish the description in the Bryologist. Williams (1924) published the description as indicated, and both the letter and the specimen are at NY. However, this specimen should not be considered type material.

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* To be validated separately

Description: Plants large-sized, robust, forming somewhat loose to densely intertwining mats; yellow-green to olive-green, often older stems and branches distinctly orange-brown to brown, dull. Stems prostrate, apices distinctly hooked; elliptic when dry or moist; not fragile when dry; outer cortical cells of 4-6 layers, orange-red, thick-walled; cells of medulla ± thin-walled, angular, gradually large-lumened, hyaline; central strand lacking. Branching irregularly, branches numerous and ± short, 2° to 3° branches numerous, usually short and somewhat erect. Rhizoids smooth; red-brown; occasional; not branching; rarely forming tufts along stems; long pendulous threads common near stem apex; rarely on branches. Paraphyllia lacking. Stem leaves densely arranged; erect-appressed when dry, spreading when moist; acumen long flexuose; distinctly concave throughout; asymmetric, distinctly falcate-secund; distinctly biplicate; narrowly long decurrent; lanceolate and gradually acuminate to a long, hyaline point, rarely somewhat short; 1.65-2.65 mm long x 0.40-0.92 mm wide, mostly 1.75-2.40 mm long x 0.65-0.86 mm wide. Branch leaves similar in shape to stem leaves, usually slightly smaller, more distinctly serrate above, with a shorter hyaline point. Margins of hyaline hair point smooth, acumen somewhat to distinctly serrate; somewhat to distinctly recurved from middle to lower acumen, somewhat recurved from mid-leaf to leaf base, sometimes more so on one side. Costa greenish-yellow; ending abruptly in lower acumen, never subpercurrent or percurrent; stout below, quickly narrowing in upper leaf proper; abaxial surface slightly keeled below, not keeled above; indistinctly or scarcely prorate along upper abaxial portion. Laminal cells mostly echlorophyllose, translucent. Alar region large, mostly extending ⅓ up leaf margin; cells thick-walled, not at all lax; quadrate to obliquely quadrate-rhomboidal, with few short-rectangular and longer cells interspersed, some oblique transverse-elongate cells interspersed; 4.8-21.6 μm long x 4.8-12.0 μm wide, mostly 7.2-12.0 μm long x 7.2-9.6 μm wide (rarely from 14.4-21.6 μm long). Basal cells thick-walled, distinctly pitted throughout; elongate-rectangular to distinctly linear, rarely quadrate cells interspersed; 12.0-62.4 μm long x 2.4-4.8 μm wide, mostly 24.0-40.8 μm long x 2.4 μm wide (rarely from 43.2-62.4 μm long). Median cells very thick-walled; distinctly pitted, rarely indistinctly so; ± homogeneous from costa to leaf margin, marginal cells sometimes smaller; somewhat to distinctly shorter than basal cells, oblong-fusiform to oblong-linear with rounded ends, sometimes smaller cells interspersed; 9.6-50.4 µm long x 4.8-7.2 µm wide, mostly 16.8-36.0 µm long x 4.8 µm wide (rarely from 38.4-50.4 µm long). Distal cells thick-walled; distinctly pitted; similar to median, somewhat rhomboidal below, becoming oblong-fusiform above; 7.2-43.4 µm long x 4.8-9.6 µm wide, mostly 16.8-31.2 µm long x 7.2 µm wide (rarely greater than 33.6 µm long). Papillae round; on upper cell lumen, often appearing somewhat prorate; median and distal cells distinctly papillose; stem and branch leaves equally distinctly papillose; papillae common on both abaxial and adaxial leaf surfaces. Perichaetia rare to occasional; lustrous and opaque; perichaetial leaves spreading, broadly lanceolate, gradually acuminate, somewhat serrate above; costa very weak and narrow, ending mid-leaf or below; basal cells lax, somewhat pitted, rectangular; median cells thick-walled, distinctly pitted throughout, fusiform-linear; distal cells thick-walled, pitted throughout, short-rhomboidal to fusiform; cells not prorate. Perigonia rare, one to few along stems, none on branches; perigonial bracts ovate-acuminate, appressed, concave, entire, apex somewhat cucullate; costa lacking; basal cells lax, somewhat pitted, oblong to long-fusiform; median cells ± thick-walled, pitted throughout, long fusiform; distal cells thick-walled, somewhat pitted, short-fusiform; papillae indistinct, on upper cell lumen, often lacking. Sporophyte rare. Seta smooth, stout; orange-red, becoming distinctly yellow-orange when old; straight or indistinctly dextrorse below, gradually somewhat sinistrorse above; 7.0-15.0 mm long. Capsule erect or somewhat inclined due to bent seta, globose-cylindric, symmetric; red-purple, becoming orange when old, distinctly smooth and lustrous; rarely slightly constricted below mouth when dry, mouth not flaring outward, remaining globose when wet; 0.8-1.7 mm long. Operculum conic, with a distinct minute nipple or apiculus. Peristome inserted along small mouth of capsule, or slightly inserted. Exostome teeth yellowish-orange below, yellow-hyaline above; lanceolate, somewhat shouldered; inflexed, rarely distinctly incurved, distal portions touching endostome segments; sometimes several teeth fused along edges; joined at base to form a yellow or yellow-orange band; proximal dorsal surface with fine horizontal striae to nearly ½ height of tooth, fine papillose-striae in median portion, fine papillae leading to sparse and rounded papillae in distal portion of tooth; apex somewhat blunt; ventral surface distinctly trabeculate; 360-590 µm long. Endostome segments yellowish, yellowish-orange, or yellowish-hyaline; as long or longer than exostome, sometimes broken off;

lanceolate, distinctly keeled, straight; widely perforate along median line; narrowly spaced, joined to form a medium basal membrane of similar colour ⅓ to ½ height of segments; dorsal and ventral surfaces somewhat sparse and minutely papillose throughout; 220-420 μm long; cilia linear, 1-2, or more often rudimentary or lacking, appendiculate. Spores minutely papillose; variable, 12.0-27.6 μm in diameter, mostly 21.6-24.0 μm in diameter. N = 8, 16 (Fritsch 1982).

Diagnostic characters: *Rigodiadelphus baileyi*, endemic to the westernmost region of North America, is a large and robust taxon. This species is predominately corticolous (on branches of small shrubs) at lower latitudes, and terricolous or sometimes saxicolous at higher latitudes. This taxon is easily identified by its olive-green colour and large habit; large falcate-secund leaves; hyaline hair point; weaker costa; and distinctly pitted laminal cells (excluding alar cells). Stems and branches, which are distinctly elliptic even when moist, lack central strands as well as paraphyllia. In addition to this, both stems and branches consist of numerous (4-6) small and thick-walled outer cortical cells. Sporophytically, *R. baileyi* has a unique capsule not found in any other taxon of *Lescuraea* in North America. The capsule is distinctly globose-cylindric, lustrous, and smooth. The operculum is conical, bearing a minute nipple or apiculus, also not seen in the other taxa.

Rigodiadelphus baileyi may be superficially confused with *Lescuraea atricha*, also endemic to western North America, due to similarly pitted laminal cells. However, *L. atricha* never has a hyaline hair point. Other differences include the presence of a central strand in *L. atricha*, paraphyllia, distinctly prorate laminal cells, and a stout abaxially prorate costa. As indicated earlier, the capsule of *R. baileyi* is so unique that it cannot be confused with that of *L. atricha*, or any other taxa in *Lescuraea*. On the other hand, *R. baileyi* can be confused both gametophytically and in part sporophytically with *Rigodiadelphus robustus* from Asia. This epiphyte also features elliptic stems and branches lacking both central strands as well as paraphyllia; numerous thick-walled outer cortical cells; leaves with hyaline hair points; weak costa ending in the lower acumen; pitted cells; capsules that are globose-cylindric, smooth, and lustrous; and an operculum with a minute nipple. However, the distinguishing feature is the reduced nature of the peristome in *R. robustus*. Where the peristome is somewhat hypnaceous in *R. baileyi*, the exostome teeth are short and mostly fused into pairs in *R. robustus*. In addition, exostome teeth of *R. robustus* are smooth or papillose throughout and not at all striate, and endostome segments are lacking. Occasionally, rudimentary nubs from highly reduced segments can be seen on the endostomal membrane. However, cilia are always lacking.

Variation: Most of the variation in *Rigodiadelphus baileyi* is in leaf length and width, 1.65-2.65 mm long x 0.40-0.92 mm wide, mostly 1.75-2.40 mm long x 0.65-0.86 mm wide, with laminal cells not highly variable between specimens. The hyaline hair point may be somewhat short or quite long.

Lawton (1957) used the fruiting specimen sent to the New York Botanical Garden by Bailey in 1924, and described the exostome teeth as "sometimes irregular," the endostome segments as "poorly developed" with the basal membrane "about one fourth the length of the outer teeth," and "cilia none or rudimentary." Having examined this specimen along with a number of fruiting specimens from several localities, Lawton's (1957) observations were not substantiated. While the exostome segments may be slightly irregular in some capsules, the endostome is never poorly developed. In addition, while cilia are often rudimentary or lacking, filiform and well-developed cilia have also been observed.

Habitat: *Rigodiadelphus baileyi* occurs predominantly on branches of shrubs and bases of trees in subalpine *Chamaecyparis-Tsuga-Abies* forests at lower latitudes (46° to 53°) although not exclusive to these forest types. This species is ccasionally found growing on soil over siliceous and alkaline boulders, rock outcrops and cliff faces, and directly on soil. In Northwestern British Columbia and throughout Alaska, this species is principally found on soil or rock in moist meadow or tundra slopes. Elevation: approximately 84-1380 metres (mostly 425-1000 m, rarely less than 300 or greater than 1200 m).

Distribution: *Rigodiadelphus baileyi* has been collected from coastal regions of northwestern, central, and southwestern British Columbia, including Vancouver Island; the northwestern portion of Washington; and from the Alexander Archipelago, Aleutian

Islands, and the coastal mainland of Alaska. One collection has been made in the northern portion of Oregon. This species is not known to occur east of the Cascade Mountains or in Asia.

Specimens examined: NORTH AMERICA: CANADA: British Columbia: Calvert Island: Slopes of Mt. Buxton – *Schofield 28037* (CANM). Coast Range of N. Vancouver: Cypress Bowl – *Steere* (NY). North Vancouver: Mount Seymour Provincial Park – *Schofield & Ramsay 71448, Krieger & Hebben 1835, 1836* (ALTA), Lion's Bay – *Schofield 19877* (CANM). E. of Pemberton: slopes of Mt. Matier – *Schofield 56878* (MO). Prince Rupert Area: Pitt Island – *Vitt 24594* (MO). Queen Charlotte Islands: Graham Island – *Schofield 15905* (US), Moresby Island – *Schofield 24885* (CANM), *Persson* (NY). Sechelt Peninsula: Karen Range – *Schofield 100497* (NY). Skeena River Area: Inver Creek – *Schofield & Sharp 25732* (CANM). Toba Inlet: Brehm River – *Scagel 80-328* (UBC). Vancouver Island: Brooks Peninsula – *Schofield 82448* (MO), Mt. Cain – *Price & Halbert 6737* (CANM), Upper Latherine Creek – *Scagel 80-2* (UBC). **USA: Alaska:** Aleutian Islands: Adak Island – *Schofield 101949* (UBC), *Schofield, Talbot, Talbot & Schofield 102259* (UBC). Izembek National Wildlife Reserve – *Schofield, Talbot & Talbot 99823* (UBC). Kodiak Island – *Sharp 188* (NY). Simeonoff Island – *Schofield 106175* (NY). Unalaska Island – *Schofield 104596* (UBC). Alexander Archipelago: Baranoff Island – *Worley, Sharpe & Iwatsuki 3922* (UBC). Chisik Island – *Talbot & Looman 87-989* (UBC). Etolin Island – *Worley & Hamilton 8278* (UBC). Juneau – *Hermann 21980* (US), *Worley & Boas 11503* (MO). Kruzof Island – *Worley & Hamilton 9629* (UBC). Kuiu Island – *Worley & Schofield 9089* (UBC). Mitkof Island – *Worley, Schofield & Hamilton 8548* (UBC). Prince of Wales Island – *Worley & Hamilton 6964* (UBC). Wrangell Island – *Worley & Hamilton 7935* (UBC). Mainland: near Sitka: vicinity of Harbor Mtn Road – *Worley & Thorpe 2967* (UBC), trail to Mt. Verstovia – *Worley & Thorpe 3344* (UBC). **Washington:** Cascade Summit – *Bailey 474* (NY – lectotype, isotypes – F, US, DUKE, MICH), *Bailey* July 13, 1916 (NY, DUKE). King Co.: near Silver Peak – *Bailey 5966* (MO). Olympic National Park: near Solduc Hot Springs – *Schofield, Ireland & Boas 19414* (UBC). Snohomish Co.: N. slope of Mt. Pilchuk – *Hermann 18458* (US). Whatcom Co.: Mt. Baker – *Conard 272* (F). Between Mt. Shuksan and Mt. Baker – *Schofield 16084* (US, NY). **Oregon:** Multnomah Co.: summit of Larch Mt. – *Ireland 6914* (CANM).

Table 2.1. *Lescuraea* and *Pseudoleskea* according to Kindberg (1897), Best (1900), and Lawton (1957) – in chronological order within publication.

Kindberg 1897	**Best 1900**	**Lawton 1957**
Lescuraea Bruch & Schimp. *in* B.S.G. **A.** *L. striata* (Hedw. *in* Schwägr.) Bruch & Schimp.*in* B.S.G. *L. saxicola* (Bruch & Schimp.*in* B.S.G.) Molendo *L. imperfecta* C. Müll. & Kindb. **B.** *L. stenophylla* (Ren. & Card.) Kindb. *L. frigida* Kindb. ***Pseudoleskea*** Bruch & Schimp. *in* B.S.G. **Subg. *Eu-Pseudoleskea*** **A.** *P. atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G. * *P. filamentosa* (Dicks. *ex* Brid.) Boulay * *P. tenella* Kindb. *P. ticinensis* Bottini *P. brachyclados* (Schwägr.) Kindb. * *P. borealis* Kindb. *P. patens* (Lindb.) Kindb. *P. heterocladioides* Kindb. **B.** *P. falcicuspis* C. Müll. & Kindb. *in* Macoun *P. oligoclada* Kindb. **Subg. Ptychodium** Schimp. **A.** *P. plicata* (Schleich. *ex* F. Weber & D. Mohr) Kindb. * *P. rhaetica* Kindb. *P. affinis* (Limpr.) Kindb. *P. hyperborea* (C. Müll.) Kindb. *P. sciuroides* Kindb. * *P. denudata* Kindb. (*) subspecies	***Pseudoleskea*** Bruch & Schimp. *in* B.S.G. **Subg. *Eu-Pseudoleskea*** Kindb. *P. atrovirens* (Dicks. *ex* Brid.) Bruch & Schimp. *in* B.S.G. *P. oligoclada* Kindb. *P. pallida* Best *P. pallida* var. *filescens* Best **Subg. *Radicosella*** Best *P. denudata* Kindb. *P. denudata* var. *holzingeri* Best *P. radicosa* (Mitt.) Lesq. & James. *P. radicosa* var *compacta* Best *P. rigescens* (Wils.) Lindb. *P. rigescens* var. *howei* Best **Subg. *Lescuraea*** (Bruch & Schimp. *in* B.S.G.) Best *P. substriata* Best	***Lescuraea*** Bruch & Schimp. *in* B.S.G. **Subg. *Pseudoleskea*** (Bruch & Schimp. *in* B.S.G.) E. Lawton *L. patens* (Lindb.) Arn. & C. Jensen *L. incurvata* (Hedw.) E. Lawton *L. incurvata* var. *gigantea* E. Lawton *L. incurvata* var. *tenuiretis* (Culm) E. Lawton *L. saviana* (DeNot.) E. Lawton *L. radicosa* (Mitt.) Mönkem. * *L. radicosa* var. *radicosa* f. *bernardensis* (Ammann) E. Lawton *L. radicosa* var. *radicosa* f. *holzingeri* (Best) E. Lawton *L. radicosa* var. *denudata* (Kindb.) E. Lawton *L. radicosa* var. *compacta* (Best) E.Lawton *L. radicosa* var. *pallida* (Best) E. Lawton *L. atricha* (Kindb.) E. Lawton *L. stenophylla* (Ren. & Card.) E. Lawton * *L. plicata* (Schleich. *ex* Web. & Mohr) E. Lawton **Subg. *Tricholeskea*** E. Lawton *L. baileyi* (Best & Grout) E. Lawton **Subg. *Lescuraea*** (Bruch & Schimp. *in* B.S.G.) E. Lawton **L. striata* (Hedw. *in* Schwägr.) Bruch & Schimp. *in* B.S.G. *L. saxicola* (Bruch & Schimp. *in* B.S.G.) Milde *L. iliamniana* E. Lawton (*) exclusive to Europe

B. **a.** *P. rigescens* (Wils.) Lindb. *P. bicolor* Kindb. *P. atricha* Kindb. **b. aa.** *P. decipiens* (Limpr.) Kindb. *P. pfundtneri* (Limpr.) Kindb. **b. bb.** *P. breidleri* Kindb.		

Table 2.2. *Lescuraea* and *Pseudoleskea* according to Brotherus (1907, 1925).

Pseudoleskea Bruch & Schimp. *in* B.S.G.

Sekt. I. *Pseudo-Pterogonium* Broth. *in* E.P.
P. imbricata (Hook. fil. & Wils.) Broth.
P. claviramea (C. Müll.) C. Müll.
P. leikipiae (C. Müll.) Par.
P. obtusiuscula Ren. & Card.
P. artariae Thér.
P. laevissima Card.
P. pseudo-attenuata (C. Müll.) Broth.
P. leskeoides (Schimp.) Broth.
P. macowaniana C. Müll.
P. capilliramea C. Müll.

Sekt. II. *Eu-Pseudoleskea* Broth. l.c. [Sect. *Eu-Pseudoleskea* Best. and Sect. *Radicosella* Best]
P. andina Schimp. (P. rusbyana C. Müll.)
* *P. patens* (Lindb.) Limpr.
P. filamentosa (Dicks.) Broth.
* *P. oligoclada* Kindb.
* *P. pallida* Best
P. laevifolia (Mitt.) Jaeg.
P. papillarioides C. Müll.
P. dispersa C. Müll.
P. peraldierii Besch.
* *P. denudata* Kindb. (Ptychodium oligocladum Limpr.)
* var. *Holzingeri* Best
P. secunda (Arn. as *Lesquereuxia*)
P. lutescens Card.
* *P. rigescens* (Wils. *ex* Par.) Lindb.
* *P. radicosa* (Mitt) Kindb. & Macoun [*P. pfundtneri* (Limpr.) Kindb.]
* *P. stenophylla* Ren. & Card.
P. decipiens (Limpr.) Kindb.

Sekt. III. Orthotheciella [C. Müll. as Sekt. *Hypnum*] Broth. *in* E.P.
P. chalaroclada (C. Müll.) Par.
P. desmioclada (C. Müll.) Par.
P. austro-catenulata (C. Müll.) Par.
P. filum (C. Müll.) Par.
P. lurida Card.
P. fuegiana (Besch.) Broth.
P. calochroa Card.
P. sordidoviridis Card. & Broth.
P. strictula Card.
P. platyphulla Card.
P. antarctica Card.

Lescuraea Bruch & Schimp. *in* B.S.G.

L. striata (Schwägr.) B.S.G.
* *L. saxicola* (B.S.G.) Mol.
* *L. substriata* (Best) Par.
L. julacea Besch. & Card.

(*) also in North America

Table 2.3. Synopsis of the nomenclatural status of taxa in *Lescuraea* Bruch & Schimp. *in* B.S.G. in North America. Taxa not examined, yet considered synonyms of accepted taxa by some authors are also included.

Taxon		Status
Hypnum implexum Brid.	= *L. incurvata*	*in synon.*
Lescuraea atricha (Kindb.) E. Lawton		
L. atrovirens var. atricha Kindb. *in* Macoun	= *L. atricha*	*in synon.*
L. frigida Kindb.	= *L. saxicola*	*in synon.*
L. iliamniana E. Lawton	= *L. saxicola*	*in synon.*
L. imperfecta C. Müll. & Kindb. *in* Macoun	= *L. stenophylla*	*in synon.*
L. incurvata (Hedw.) E. Lawton		
L. incurvata* var. *incurvata (Hedw.) E. Lawton		
L. incurvata* var. *gigantea E. Lawton		
L. incurvata* var. *tenuiretis (Culm.) E. Lawton		
L. julacea Besch. & Card. *in* Card.	= *L. saxicola*	*in synon.*
****L. mutabilis*** (Brid.) Hagen		
L. patens (Lindb.) Arn. & C. Jens.		
L. radicosa (Mitt.) E. Lawton		
L. radicosa* var. *radicosa (Mitt.) E. Lawton		
L. radicosa* var. *compacta (Best) E. Lawton		
L. radicosa* var. *denudata (Kindb. *in* Macoun & Kindb.) E. Lawton		
L. radicosa var. pallida (Best) E. Lawton	= *L. radicosa* var. *compacta*	*in synon.*
L. saviana (DeNot.) E. Lawton		
L. saxicola (Bruch & Schimp. *in* B.S.G.) Molendo *in* Lorentz		
L. stenophylla (Ren. & Card.) E. Lawton		
Leskea brachyclados Schwägr. *in* Schultes	= *L. radicosa*	*in synon.*
Pseudoleskea bicolor Kindb.	= *L. radicosa*	*in synon.*
P. denudata var. Holzinger Best	= *L. radicosa*	*in synon.*
P. falcicuspis C. Müll. & Kindb. *in* Macoun & Kindb.	= *L. incurvata*	*in synon.*
P. heterocladioides Kindb.	= *L. patens*	*in synon.*
P. illyrica Glow.	= *L. saviana*	*in synon.*
P. jemtlandica Kindb.	= *L. radicosa*	*in synon.*
P. oligoclada Kindb. *in* Macoun	= *L. incurvata*	*in synon.*
P. sciuriodes Kindb. & Macoun *in* Macoun	= *L. radicosa*	*in synon.*
P. substriata Best	= *L. saxicola*	*in synon.*

Ptychodium decipiens Limpr.	= *L. saxicola*	*in synon.*
Ptychodium oligocladon Limpr.	= *L. radicosa* var. *denudata*	*in synon.*
Ptychodium pfundtneri Limpr.	= *L. radicosa*	*in synon.*

(*) exclusive to Europe

Insufficiently known taxa

Brachythecium perrevolutum Broth *ex* Iisiba	= *L. saxicola*, fide Iwatsuki 1991	type not seen
Hypnum atrovirens Brid.	= *L. incurvata*, fide Ignatov & Afonina 1992	type not seen
H. attenuatum Dicks. *ex* With.	= *L. incurvata*, fide Wijk et al. 1964	type not seen
H. filamentosum Dicks. ex With.	= *L. incurvata*, fide Wijk et al. 1964	type not seen
H. mutabile Brid.	= *L. mutabilis*, fide Wijk et al. 1964	type not seen
H. radicosum var. gracilis Lesq. & James	= *L. stenophylla*, fide Wijk et al. 1964	type not seen
Lescuraea iwasakii Iwas.	= *L. mutabilis*, fide Iwatsuki 1991	type not seen
Pseudoleskea atrovirens var. acutifolia Velen	= *L. saviana*, fide Wijk et al. 1967	type not seen
P. radicosa var. meridionalis Culm. *in* Amann	= *L. saviana*, fide Wijk et al. 1967	type not seen
P. ticinensis Bott.	= *L. patens*, fide Wijk et al. 1967; Redfearn Jr.1986	type not seen
Ptychodium abbreviatum Amann	= *L. mutabilis*, fide Wijk et al.1967; Redfearn Jr. 1986	type not seen

Table 2.4. *Nomina invalida*, *nomina illegitima*, *nomina nuda*, and orthographic variations in *Lescuraea*.

Nomina invalida

Taxon	Status	
Lescuraea filamentosa var. subcatenulata Sael. *ex* Par.	*nom. inval. in synon. err. pro*	= *Lescuraea incurvata*
L. filamentosa var. subnitidula Lindb. *ex* Par.	*nom. inval. in synon. err. pro*	= *Lescuraea incurvata* var. *subnitidula*
L. striata var. julacea (Besch. & Card.) Besch. *ex* Toyama	*nom. inval. in syon.*	= *Lescuraea saxicola*
Pseudoleskea catenulata var pseudo-tectorum Par.	*nom. inval. incl. var. prior.*	= *Pseudoleskeella tectorum*
P. decurvata var. annamensis (Broth. & Par.) Thér. *ex* Dix.	*nom. inval. in synon. err. pro*	= *Pseudoleskeopsis zipelii*
P. falcata Schimp. *ex* Par.	*nom. inval. in synon. err. pro*	= *Lescuraea saxicola*
P. radicosa var. gracilis Lesq. & Jam. *ex* Macoun & Kindb.	*nom. inval. in synon. err. pro*	= *Lescuraea stenophylla*
P. pterocladioides Kindb. *ex* Podp.	*nom. inval. in synon. err. pro*	= *Lescuraea patens*

***Nomina illegitima* and orthographic variations**

Taxon	Status	
Lescuraea breidleri (Kindb.) Arn. & C. Jens.	*nom. illeg. incl. spec. prior*	= *Lescuraea radicosa* var. *denudata*
L. denudata (Kindb.) Mönkem.	*nom. illeg. incl. spec. prior*	= *Lescuraea radicosa* var. *denudata*
L. mutabilis var. eu-mutabilis Podp.	*nom. illeg. incl. spec. prior*	= *Lescuraea mutabilis*
L. striata (Schwägr.) B.S.G.	*nom. illeg. incl. spec. prior*	= *Lescuraea mutabilis*
Lesquereuxia patens Lindb.	*ortho. pro*	= *Lescuraea patens*
L. saxicola ssp. striata (Schwägr.) Kindb.	*nom. illeg. prior. ut spec.*	= *Lescuraea saxicola*
Pseudoleskea atrovirens ssp. eu-atrovirens Giac.	*nom. illeg.*	= *Lescuraea incurvata*
P. atrovirens ssp. tenella Kindb.	*hom. illeg.*	= *Lescuraea incurvata* var. *tenella*
P. congesta B.S.G. ex Paris	*nom. illeg. incl. spec. prior*	= *Lescuraea radicosa*
P. incurvata var. saviana (De Not.) Podp.	*nom. illeg. incl. var. prior.*	= *Lescuraea saviana*
P. liebmanni B.S.G. ex Par.	*nom. illeg. incl. spec. prior.*	= *Rauiella lagoensis*
P. radicosa ssp. eu-radicosa Giac.	*nom. illeg.*	= *Lescuraea radicosa*
P. radicosa var. brachyclados (Schwägr.) Podp.	*nom. illeg. prior. ut spec.*	= *Lescuraea radicosa*
P. rigescens Lindb.	*nom. illeg. incl. spec. prior.*	= *Lescuraea stenophylla*
P. tenella Kindb. ex Par.	*nom. inval. in synon. err. pro*	= *Lescuraea incurvata* var. *tenella*

Nomina nuda	**Status**	
Lescuraea brachycladula Broth. *in* Sak.	*nom. nud. in synon.*	= *Lescuraea mutabilis*
L. brevifolia Broth.	*nom. nud. in synon.*	= *Lescuraea mutabilis*
L. striata var. julacea (Besch. & Card.) Besch. & Toyama	*nom. nud. in synon.*	= *Lescuraea saxicola*
L. striata var. saxatilis Vent.	*nom. nud.*	= *Lescuraea saxicola*
Leskea rigescens Wils in B.S.G.	*nom. nud.*	= *Lescuraea stenophylla*
Lesquereuxia rigescens Lindb.	*nom. nud. in synon.*	= *Lescuraea stenophylla*
Pseudoleskea amblystegioides C. Müll. in Polak.	*nom. nud.*	
P. atrovirens var. saxicola Schimp. in Roth.	*nom. nud. in synon.*	= *Lescuraea saxicola*
P. calochroa Cardot	*nom. nud.*	= *Orthotheciella varia*
P. capensis Schimp. in Jaeg.	*nom. nud.*	
P. carbonarai Broth. in Micheletti	*nom. nud.*	
P. claviramea var. acuminata C. Müll. in Par.	*nom. nud.*	
P. claviramea var. aquatica Rehm. in Par.	*nom. nud.*	
P. costaricensis C. Müll. in Polak.	*nom. nud.*	
P. erythraea C. Müll. in Briz.	*nom. nud. in synon.*	
P. fuegiana var. fuscifolia C. Müll. in Bruehl.	*nom. nud.*	
P. integrifolia Dix. et Bartr. in Grout	*nom. nud. in synon.*	= *Pseudoleskeella arizonae*
P. japonica Geh. in Reim.	*nom. nud. in synon.*	= *Haplocladium angustifolium*
P. laxifolia Rehm. in Kindb.	*nom. nud.*	
P. macowani Rehm. in Kindb.	*nom. nud.*	= *Lescuraea leskeoides*
P. pterogonioides Broth. in Bruehl.	*nom. nud.*	= *Bryonorrisia acutifolia*
P. subfalcata Schimp. in Mild.	*nom. nud. in synon.*	= *Lescuraea mutabilis*
P. vagans C. Müll. in Bruehl.	*nom. nud.*	

Table 2.5. Excluded names from *Lescuraea*. The following are considered species of other genera.

Lescuraea chilensis Herzog, Rev. Bryol. Lich. 23: 87. 24. 1954.
Type: "Mittelchile: Cuesta La Dormida, 1.030 m., auf Erde, leg. G.H. SCHWABE, n° 140/b. **Holotype – JE !**

Herzog (1954) originally described this species from Chilean material. Herzog indicated that this species is similar to *Lescuraea decipiens* (= *L. saxicola*, *fide* Wijk *et al.*, 1964) in the narrow laminal cells. However, he distinguished *L. chilensis* from the latter in having broader leaves, much narrower laminal cells, and in having a broader alar region. Examination of the type material indicates that this specimen does not belong in *Lescuraea*. The leaf margins are serrate throughout, and not at all recurved. The alar cells, which are round or irregular, become inflated below and cannot be distinguished from the basal cells. The leaf decurrencies also consist of inflated cells. Laminal cells are smooth throughout, and paraphyllia are lacking on both stems and branches. In addition, the costa is smooth throughout, and slightly forked below. This specimen resembles *Hygroamblystegium tenax* var. *spinifolium* (Schimp.) Jenn.

Lescuraea darjeelingensis Vohra, Bull. Bot. Surv. India 20: 150. pl. 1. 1978 [1979].
Type: "Type – India. Darjeeling, Tongloo, Batashi Road, 3060 m *Wadhwa 166*. Bhutan. *Wadhwa 32*. **Holotype – CAL** (not seen); **paratype – CAL !** (*Wadhwa 32*)

Vohra described *Lescuraea darjeelingensis* for a specimen collected by Wadhwa in Darjeeling, India. He also listed a paratype, collected by the same person. Unfortunately, only the paratype was received on loan from CAL. The plant habit appears similar to that of *Lescuraea*, although examination of the paratype reveals that this is not *Lescuraea*. There are clearly no paraphyllia along stems and branches, the alar region is very small (3-4 cells across and high), alar and many basal cells are clearly inflated, laminal cells are extremely linear, and the costa is weak, narrow, not at all keeled or prorate, and ends mid-leaf. I have no suggestions of synonymy at this point. However, the holotype should be examined before any definitive conclusions are made.

Lescuraea serrata Warnst., Hedwigia 57: 110. 44. 1915.
Type: "Italien: Viareggio bei Pisa, an Bäumen im Pinienwald im Juli 1905 leg. Kalkhoff." **Holotype – B !**

Warnstorf (1915) described this species as differing superficially from *Lescuraea saxicola* in having leaf margins that are serrate and plane throughout, and in the extensive alar region. He also indicated that paraphyllia are foliose, yet never cleft or branched. Examination of the sterile material indicates that there are no paraphyllia, but rather what Warnstorf described were pseudoparaphyllia around branch primordia. The laminal cells are not at all like those of taxa in *Lescuraea*, and the costa is smooth throughout. At the tip of the costa is a sharp spine. Based on comparisons with herbarium material at ALTA, I believe that this is *Eurhynchium praelongum* (Hedw.) Schimp. *in* B.S.G.

Pseudoleskea andina Schimp. *ex* Britt., Bull. Torr. Bot. Cl. 23: 498. 1896.
Type: [Bolivia] "Prov. Larecaja, vicinius sorata, 3200 metr. November, 1857 (1694), legit, G. Mandon "super arbores." Sorata, 13000 ft. February, 1886 (3181), H.H.R. and Unduavi, 12000 ft. October, 1885 (3180)." **Syntypes – BM !** (*Mandon 1694, 3181*)

Schimper (1896) described this species from several specimens with sporophytes. Upon examination of all three Bolivian specimens, it is apparent that this species does not belong in *Lescuraea*. These autoicous plants are highly branched, with 3° branches common. Paraphyllia are foliose as well as filamentous and highly branched. The cells of the paraphyllia are also distinctly papillose. The most notable feature is the dissimilarity in shape and size between stem and branch leaves. Based on these, as well as other characters, I believe that these specimens are *Bryohaplocladium microphyllum* (Hedw.) Watanabe & Iwatsuki.

Pseudoleskea arizonae Williams, Bryologist 33: 20. Pl. 3. 1930.
Type: "collected on north slope of Monument Peak, Chiricahua Mts., Southeast Arizona at 8300 ft., by J.C. Bloomer, Oct. 2, 1908." [NEW YORK BOTANICAL GARDEN, NEW YORK CITY]. **Holotype – NY !**

According to Williams (1930), this "species appears to be quite distinct in its dioicous inflorescence, smooth leaf cells, large annulus, long, slender cilia, and absence of paraphyllia." Having examined the type as well as a number of other specimens from the southwestern United States, it is evident that this species does not belong in *Lescuraea*. The annulus as well as the long, slender cilia are evident on all specimens with sporophytes. In addition, both stems and branches are completely devoid of any paraphyllia. Other features common to these specimens are the smooth leaf cells and smooth, often forked costae. The presence of: an annulus around the capsule mouth; long, slender cilia; absence of paraphyllia; smooth leaf cells; and a smooth forked costa, are characteristic of taxa in *Pseudoleskeella*. Lawton (1957) made the new combination, *Pseudoleskeella arizonae* (Williams) E. Lawton presumably based on these characters; unfortunately, she does not supply any reasons. Wilson and Norris (1989), in their revision of *Pseudoleskeella* and *Leskeella*, indicate that specimens of this taxon are too large to be in *Pseudoleskeella*. They also point to strips of cells on stems as remnants of paraphyllia, thereby supporting their decision for the new combination *Lescuraea arizonae* (Williams) Wilson & Norris. Having examined a number of specimens from different localities, including the type, I could find no such strips of cells. I presume that Wilson and Norris may have mistaken leaf decurrencies for paraphyllia, since they often remain attached to the stem after the leaf is removed. In addition, having compared the size of the specimens with taxa in both *Lescuraea* and *Pseudoleskeella*, they are no larger than many specimens typically found in certain taxa of *Pseudoleskeella*. Due to the similarity in characters between this taxon and taxa within *Pseudoleskeella*, I am confident following Lawton in reassigning *Pseudoleskea arizonae* to *Pseudoleskeella*.

Pseudoleskea falcifolia Dix. & Thér., Rev. Bryol. Lich. 12: 75. 1942.
Type: "Butagu, Ruvenzori, 1.800 m., leg. D^r Bequaert, n^o 73, April 1914 (type). Uganda, Bulago, on rocks below waterfall, 2.000 m., leg. Miss M. Budd, n^o 31, 1928. Uganda, Butandika, on tree, 1.800 m., leg. Miss M. Budd, n^o 42^a,1928." **Lectotype – BM !** (lectotypus); **isotype – PC !; paratypes** (not seen).

From the sterile specimens that Dixon and Thériot (1942) used to describe this taxon, it seems clear that this species does not belong in *Lescuraea*. The autoicous plants are distinctly pinnate to bipinnately branched and the stem and branch leaves are greatly dissimilar in shape and in size. The filamentous paraphyllia are distinctly papillose, and the perichaetial leaves are highly plicate throughout. Based on comparisons with herbarium material at ALTA, I believe that these specimens are *Thuidium sparsifolium* (Mitt.) Jaeg.

Pseudoleskea laevifolia (Mitt.) Jaeg., Ber. S. Gall. Naturw. Ges. 1876-77: 243. 1878.
Basionym: Leskea laevifolia Mitt., J. Proc. Linn. Soc., Bot. Suppl. 1: 1-171. 1859. **Type:** "*Hab.* In Himalayae occidentalis reg. Temp., Jamu, *T. Thomson*! (No. 1127, 1165). **Lectotype – NY !** (*Thomson 1127*, lectotypus); **syntype – NY !** (*Thomson 1165*)

According to Mitten (1859), this species resembles *Lescuraea catenulatae* (= *Pseudoleskeella catenulata*). After examination of both sterile specimens from NY, the distinguishing characters of *Pseudoleskeella* are evident. I believe that this taxon belongs in either *Pseudoleskeella* or *Leskeella*.

Pseudoleskea obtusiuscula Ren. & Card., Prodr. Fl. Bryol. Madag. Suppl. 82: 22 f. 3. 1909. **Type:** "*Madagascar:* Fianarantsoa, ad truncos, Rev. VILLAUME, 1904, (Hb. Lacouture)." **Holotype – PC !**

Renauld and Cardot (1909) described this species from a specimen collected by Rev. Villaume in Madagascar. Upon investigation of this specimen, it was immediately obvious that this specimen does not belong in the Leskeaceae. Based on gametophytic and sporophytic characters, this specimen is clearly *Levierella fabroniacea* C. Müll. A specimen examined from BM (hb. Renauld) is identical to the type material at PC.

Pseudoleskea papillarioides C.Müll. Nuov. Giorn. Bot. Ital. N. ser. 3: 118. 1896.
Type: "*Habitatio.* In medio monte Kuan-tou-san, Jul. **Holotype – BM !; isotype – H !**

The sterile specimen collected by Giraldi (no. 907) and described by Carl Müller (1896), as *Pseudoleskea papillarioides* is clearly synonymous with *P. laevifolia*. Due to the sterile nature of the specimen, I cannot specify whether it should belong in *Pseudoleskeella* or *Leskeella*.

Pseudoleskea ramuligera (Mitt.) Sauer. & Jaeg., Ber. S. Gall. Naturw. Ges. 1877-78: . 475. 1880. **Basionym:** Leskea ramuligera Mitten, J. Proc. Linn. Bot. Soc. Suppl. 1: 132. 1859. **Type:** "*Hab.* In Nepal, *Wallich!* In Kumaon, *Strachey et Winterbottom*!" **Lectotype – NY !** (lectotypus); **syntype – NY !**

Mitten (1859) described this species from material collected by Wallich, and from Strachey and Winterbottom. Examination of type material from NY clearly indicates that these specimens do not belong in the Leskeaceae. Along with the autoicous condition, stem and branch leaves are dissimilar to each other in shape and size, the cells of the paraphyllia are distinctly papillose, and the highly branched paraphyllia are crowned with multiple papillae. Comparison with material at ALTA, as well as from literature sources, reveals that these specimens are *Thuidium sparsifolium* (Mitt.) Jaeger. Koponen (1990) synonymized *T.*

rubiginosum and *T. fuscatum* (tentatively), with *T. sparsifolium*. However, the latter name was described and published by Mitten in the same article as that of *Leskea ramuligera*. Based on the International Code of Botanical Nomenclature (2000), species names published in earlier articles have priority over those that are later described, even within the same month. Unfortunately, no clear indication of priority is mentioned for species names published by an author within the same article. Theoretically, Mitten's (1859) epithet *ramuligera*, described on page 132 of his 'Mosses of the East Indies', should take priority over his later described name *sparsifolium* (on page 135). Further investigation of the species in *Thuidium* should reveal if *Leskea ramuligera* is truly synonymous with *T. sparsifolium*, and which name has priority.

Pseudoleskea setschwanica Broth., Sitz. Kaiserl. Akad. Wiss. Wien., Math.-naturw. Kl. Abt. 1, 133: 579. 1924. **Type:** "protologue unavailable" **Isotype ?– H!**

Brotherus described *Pseudoleskea setschwanica* in 1924. Cao Tong (1999) examined this specimen and indicated on the packet that it resembled *Herpetineuron toccoae* (Sull. & Lesq.) Cardot. Current examination reveals that this specimen does not belong in the Leskeaceae, although I cannot confirm its placement in *Herpetineuron*.

Pseudoleskea yuennanensis Broth., Sitz. Kaiserl. Akad. Wiss. Wien., Math.-Naturw. Kl. Abt. 1, 133: 579. 1924. **Type:** "protologue unavailable" **Isotype ? – H !**

Brotherus (1924) also described *Pseudoleskea yuennanensis* in the same article as that of the previous species. Examination of sterile type material from H indicates that this specimen is synonymous with *Pseudoleskea laevifolia* and *P. papillarioides*. All of these specimens appear to belong in *Pseudoleskeella* or *Leskeella*. Further research will be able to determine the correct placement of these specimens.

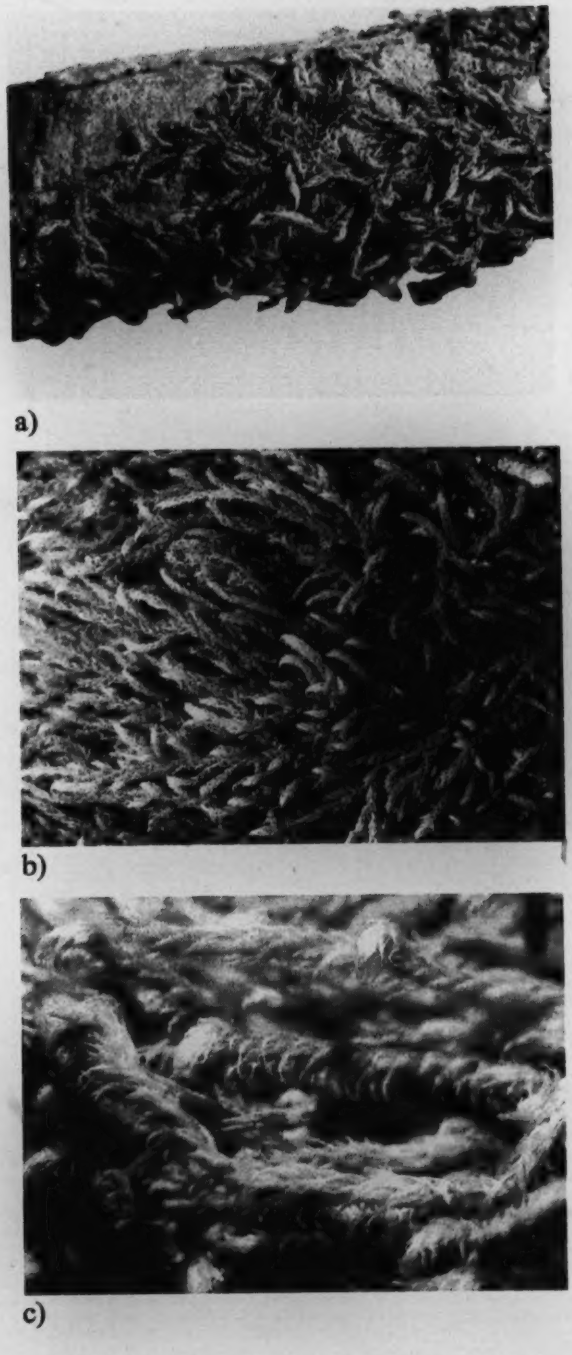

Figure 2.1. Digital images of plant size variation in *Lescuraea*: a) small plants of *L. stenophylla* (*Krieger & Hebben 1801* ALTA); b) medium plants of *L. incurvata* var. *incurvata* (*Krieger & Hebben 1807* ALTA); c) large plants of *L. radicosa* var. *denudata* (*Krieger 1563* ALTA). Images taken at 60X Mag.

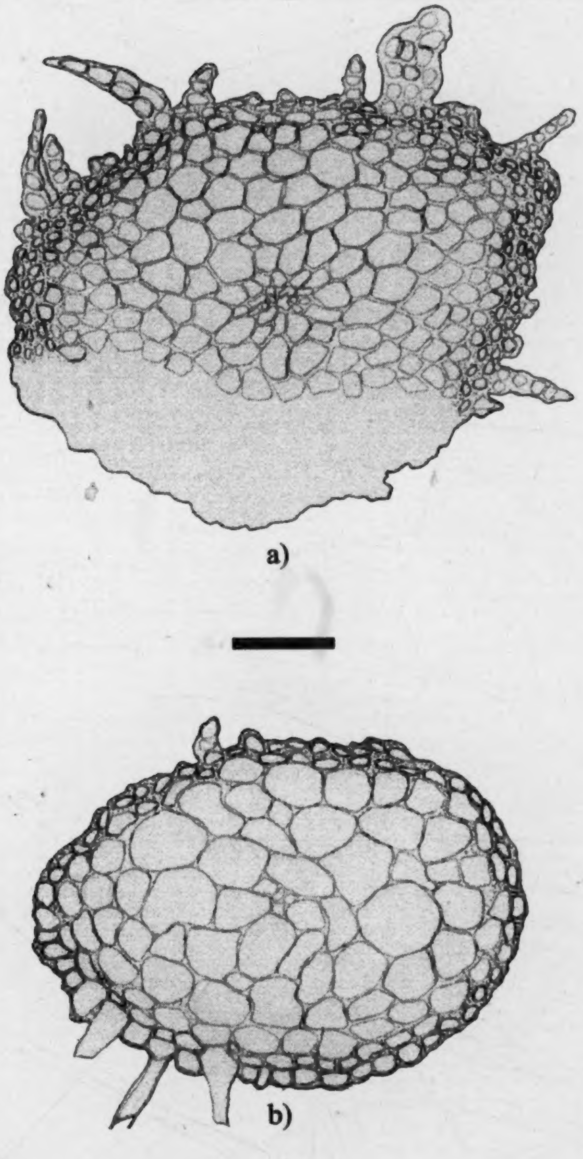

Figure 2.2. Illustrations of stem transverse section variation in *Lescuraea*: a) several rows of outer cortical cells with angular cells in medulla in *L. incurvata* (*Buck 30362* NY); b) one to two rows of outer cortical cells with rounded cells in medulla in *L. stenophylla* (*Schofield, Belland & Clayden 88386* UBC). Scale bar = 48 µm.

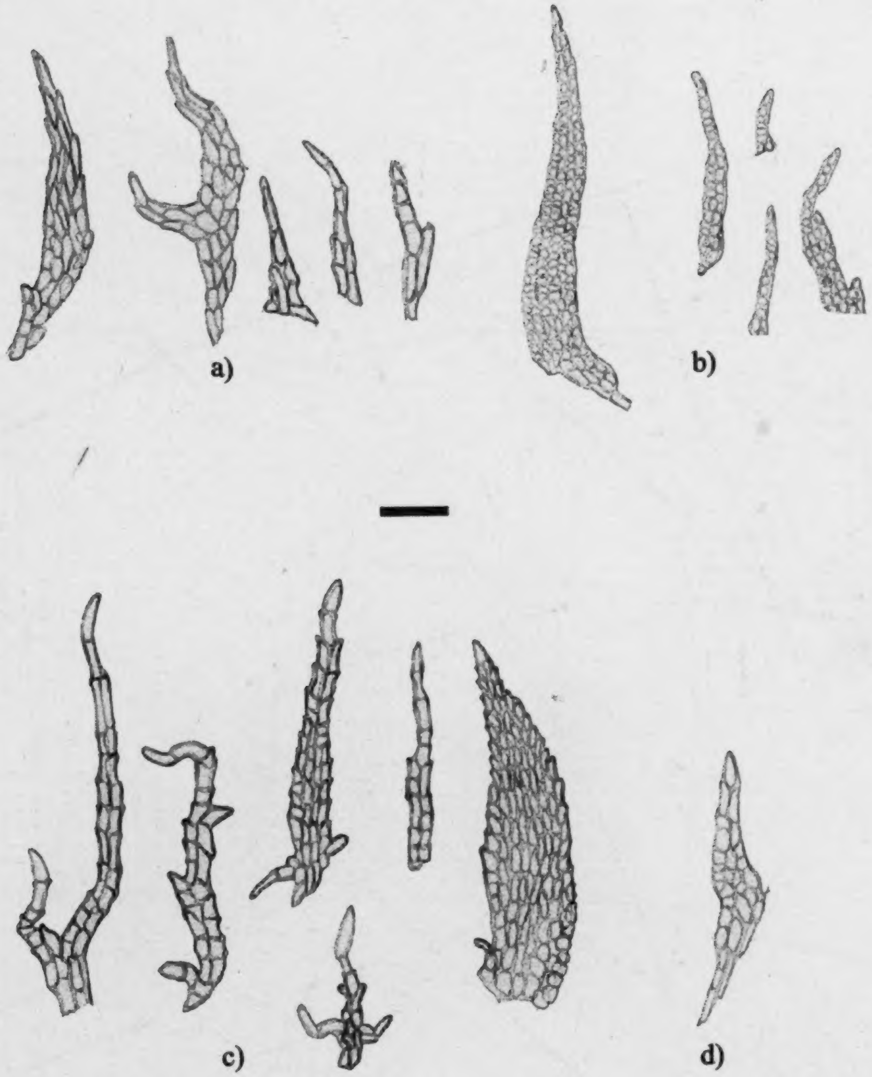

Figure 2.3. Illustrations of paraphyllia variation in *Lescuraea*: a),b) foliose and filamentous paraphyllia in *L. saxicola* (*Belland 4177* UBC) and *L. incurvata* var. *gigantea* (*Schofield & Boas 21084* UBC); c) foliose and filamentous branched paraphyllia in *L. radicosa* var. *denudata* (*MacFadden 17981* MO); d) foliose paraphyllium of *L. stenophylla* (*Schofield, Belland, & Clayden 88386* UBC). Scale bar = 48 µm.

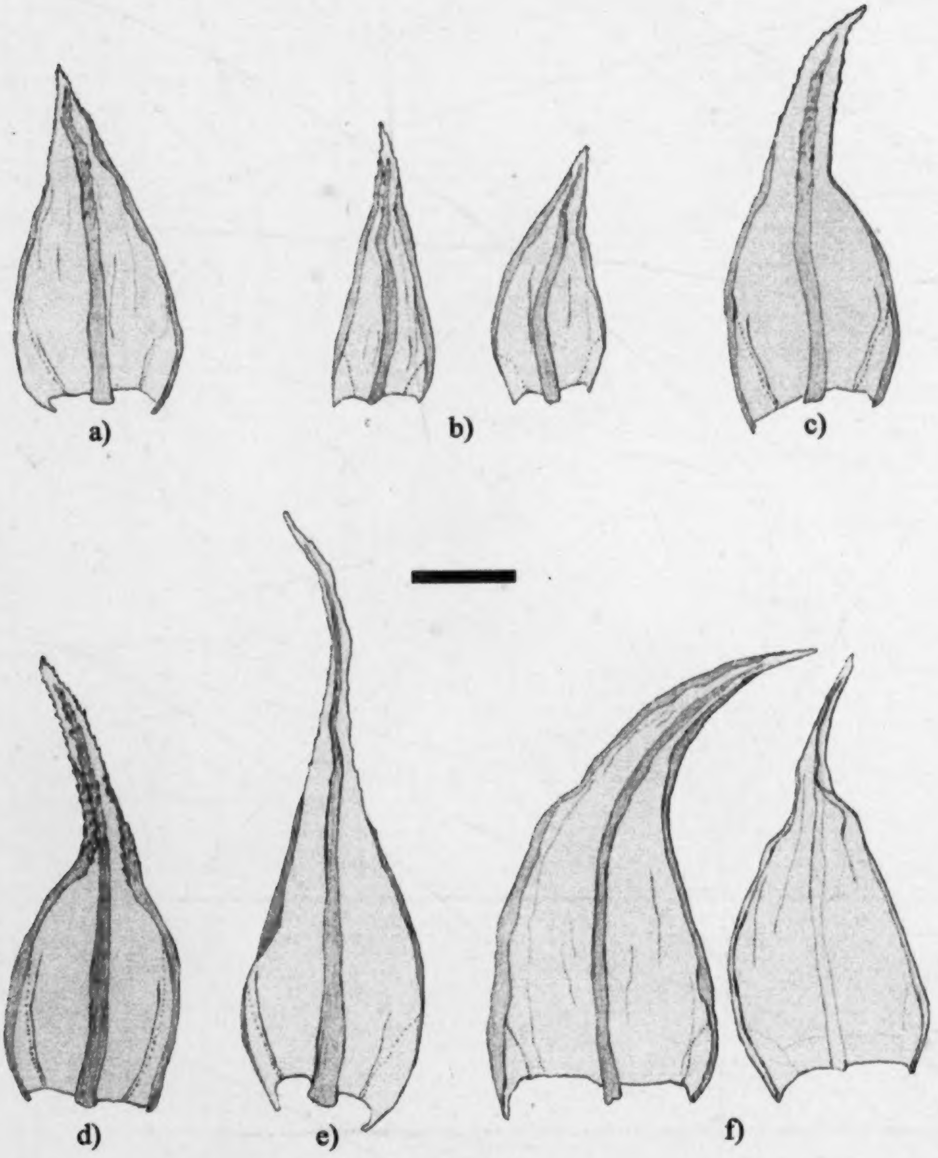

Figure 2.4. Illustrations of stem leaf shape variation in *Lescuraea*: a),b) ovate-acute leaves in *L. atricha* (*von Velzen & Leong 302.8069* UBC) and *L. saxicola* (*Stφrmer* UBC); c),d) ovate, abruptly long acuminate leaves in *L. incurvata* var. *incurvata* (*Ireland 6618* US) and *L. saviana* (*Baumgartner 1226* CANM); e),f) gradually long acuminate leaves in *L. stenophylla* (*Hasselbach* ALA) and *L. radicosa* var. *denudata* (*Macoun* S;lectotype). Scale bar = 316 μm.

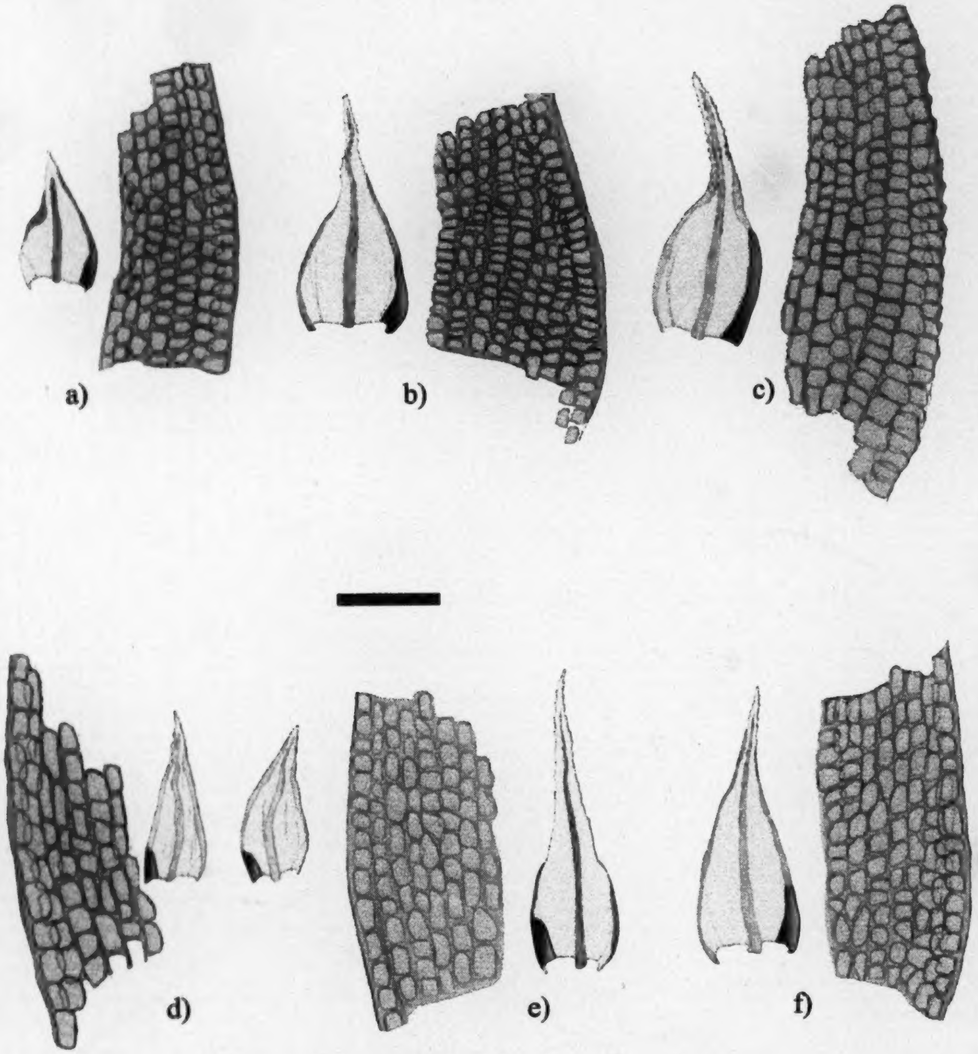

Figure 2.5. Illustrations of alar region variation in *Lescuraea*: a),b) medium alar regions in *L. patens* (*Krieger 1834* ALTA) and *L. incurvata* var. *incurvata* (*Müller 1850* UC/JEPS); c) large alar region in *L. saviana* (*Boros 4691* COLO); d),e),f) small alar regions in *L. saxicola* (*Ireland & Bellilio-Trucco 18679* F), *L. stenophylla* (*Harpel 12796* WTU), and *L. radicosa* var. *radicosa* (*Ireland 6010* WTU), respectively, Scale bar = 316 µm for leaves; 48 µm for alar cells.

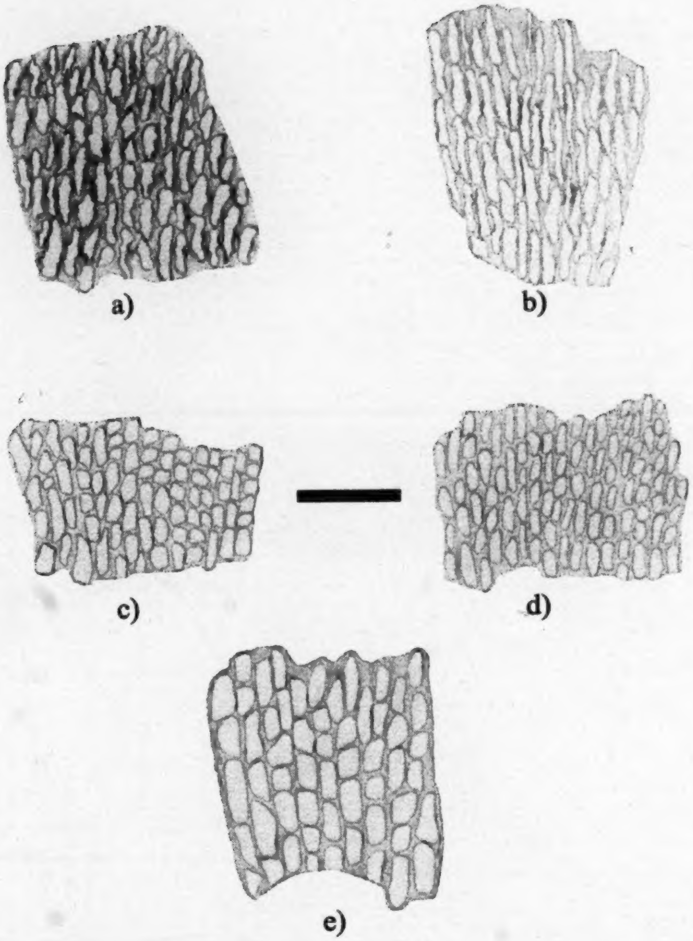

Figure 2.6. Illustrations of basal cell variation in *Lescuraea*: a),b) fusiform to linear, distinctly pitted thick-walled cells in *L. atricha* (*VanVelzen & Leong 302.8069* UBC) and *L. saxicola* (*Ireland & Bellilio-Trucco 18679* F); c),d) quadrate to elongate, thick-walled cells in *L. incurvata* var. *incurvata* (*Ireland 6618* US) and *L. incurvata* var. *gigantea* (*Krieger & Hebben 1865* ALTA); e) enlarged quadrate to rectangular, thin-walled cells in *L. radicosa* var. *radicosa* (*Hermann 24802* WTU). Scale bar = 48 µm.

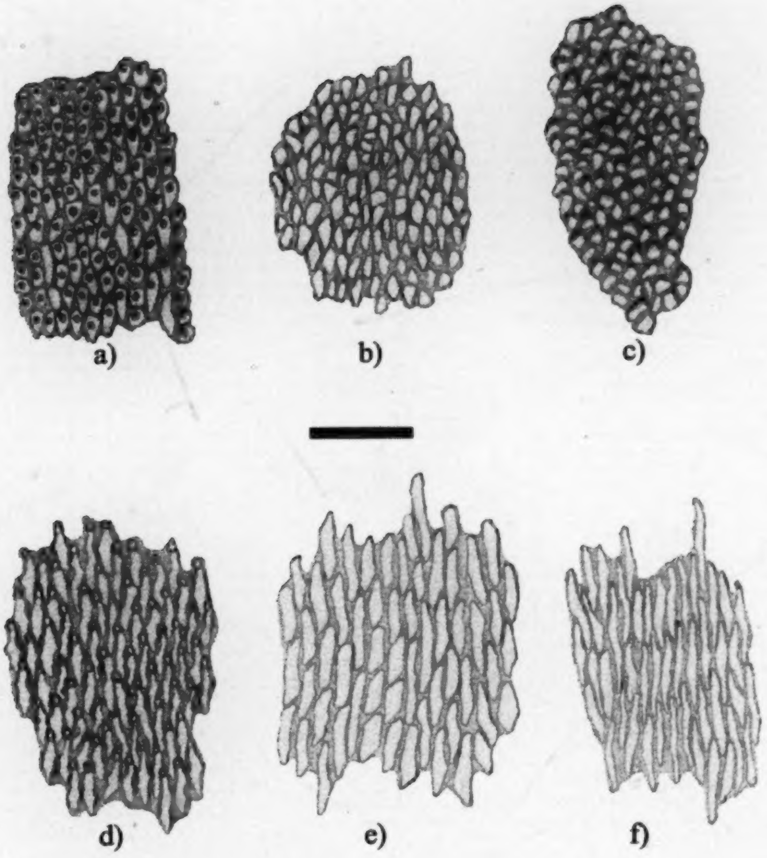

Figure 2.7. Illustrations of median cell variation in *Lescuraea*: a) isodiametric to rhombic cells with central papillae in *L. patens* (*Krieger 1834* ALTA); b),c) elliptic to angular cells in *L. incurvata* var. *incurvata* (*Ireland 6618* US) and *L. incurvata* var. *tenuiretis* (*McCune 4720* OSC/ORE); d) fusiform, distinctly pitted and prorate cells in *L. atricha* (*VanVelzen & Leong 302.8069* UBC); e) fusiform-linear, slightly prorate, pseudo-pitted cells in *L. radicosa* var. *radicosa* (*Hermann 24802* WTU); f) linear, slightly prorate cells in *L. saxicola* (*Ireland & Bellilio-Trucco 18679* F). Scale bar = 48 μm.

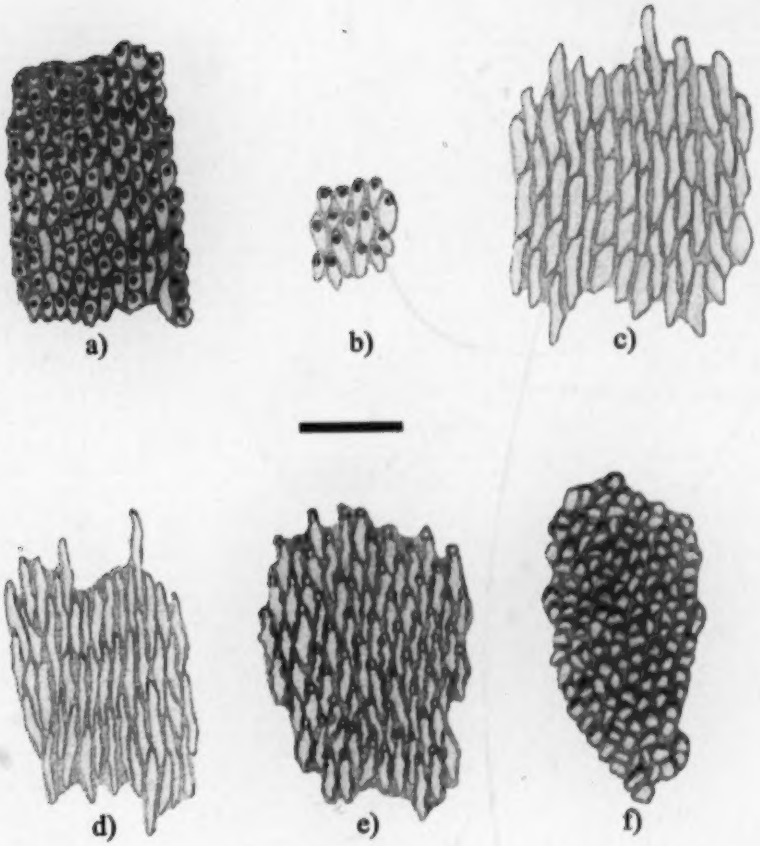

Figure 2.8. Illustrations of papillae and prorae variation in *Lescuraea*: a) central papillae in *L. patens* (*Krieger 1834* ALTA); b) papillae over upper cell lumen in *L. stenophylla* (Harpel *12796* WTU); c),d) indistinctly prorate in *L. radicosa* var. *radicosa* (*Hermann 24802* WTU) and *L. saxicola* (*Ireland & Bellilio-Trucco 18679* F); e) distinctly prorate in *L. atricha* (*VanVelzen & Leong 302.8069* UBC); f) cell lumen extending obliquely into prorae in *L. incurvata* var. *tenuiretis* (*McCune 4720* OSC/ORE). Scale bar = 48 µm.

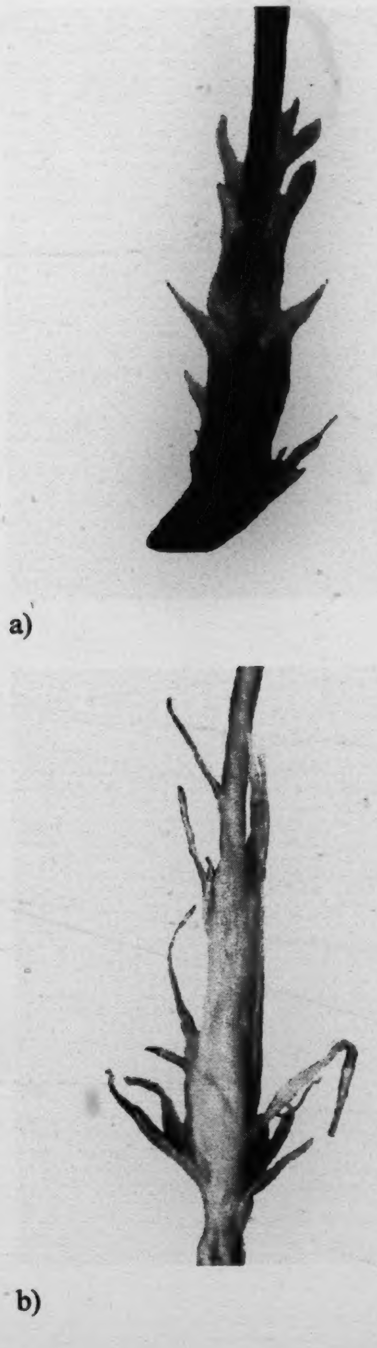

Figure 2.9. Digital images of perichaetial leaf stance variation in *Lescuraea*: a) recurved perichaetial leaves in *L. saxicola* (*Berggren 162* US); b) erect perichaetial leaves in *L. saviana* (*Boros 4691* US). Images taken at 60X Mag.

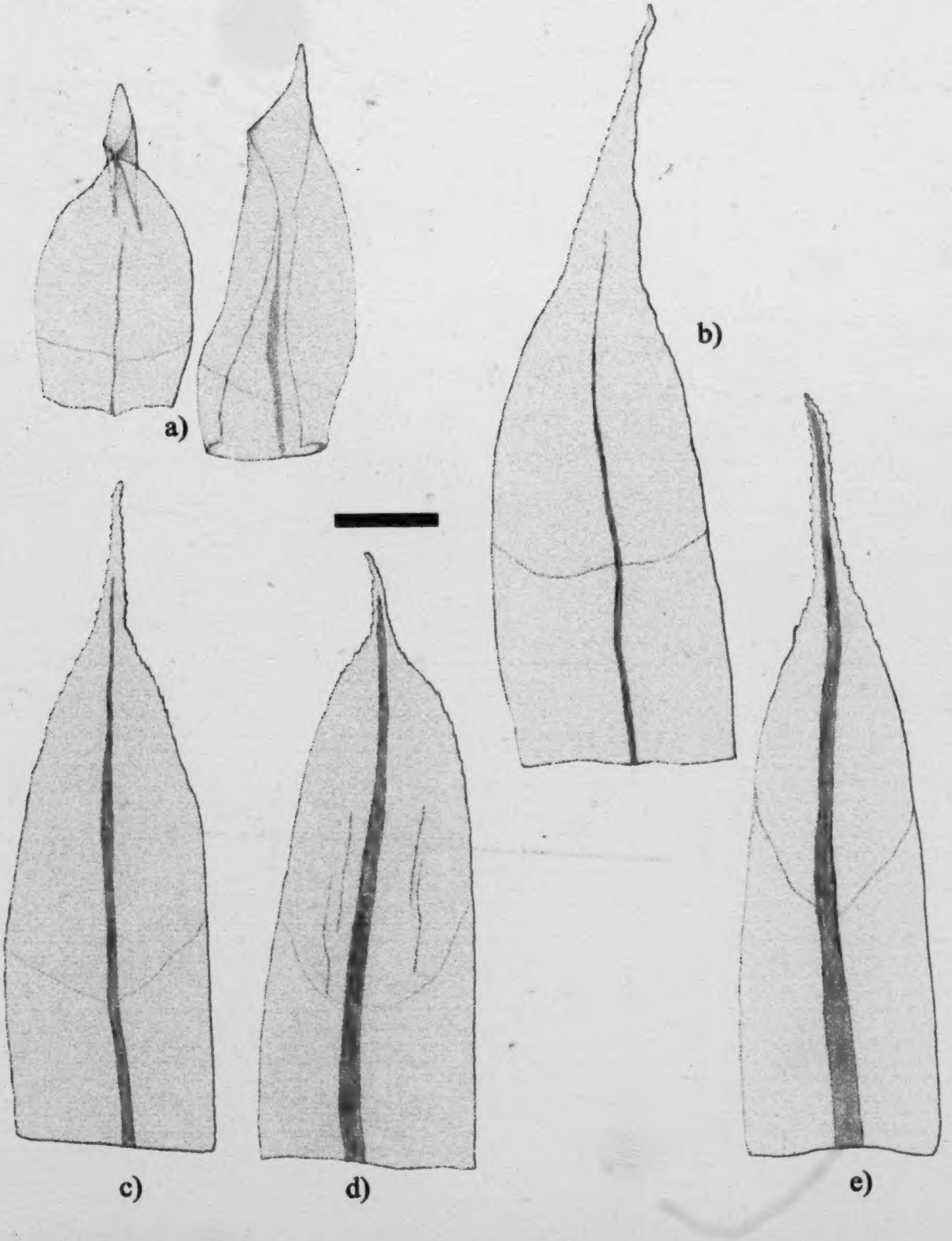

Figure 2.10. Illustrations of perichaetial leaf variation in *Lescuraea*: a) broad and ovate-acuminate leaves with weak costa of *L. saxicola* (*Iwatsuki 1011* UBC); b),c) lanceolate leaves with somewhat strong costa of *L. radicosa* var. *radicosa* (*Hermann 20581* WTU) and *L. incurvata* var. *incurvata* (*Ludwig* G); d),e) linear-lanceolate, abruptly short or long acuminate leaves with strong costa of *L. atricha* (*Frye 546* WTU) and *L. saviana* (*Baumgartner 1226* CANM). Scale bar = 316 μm.

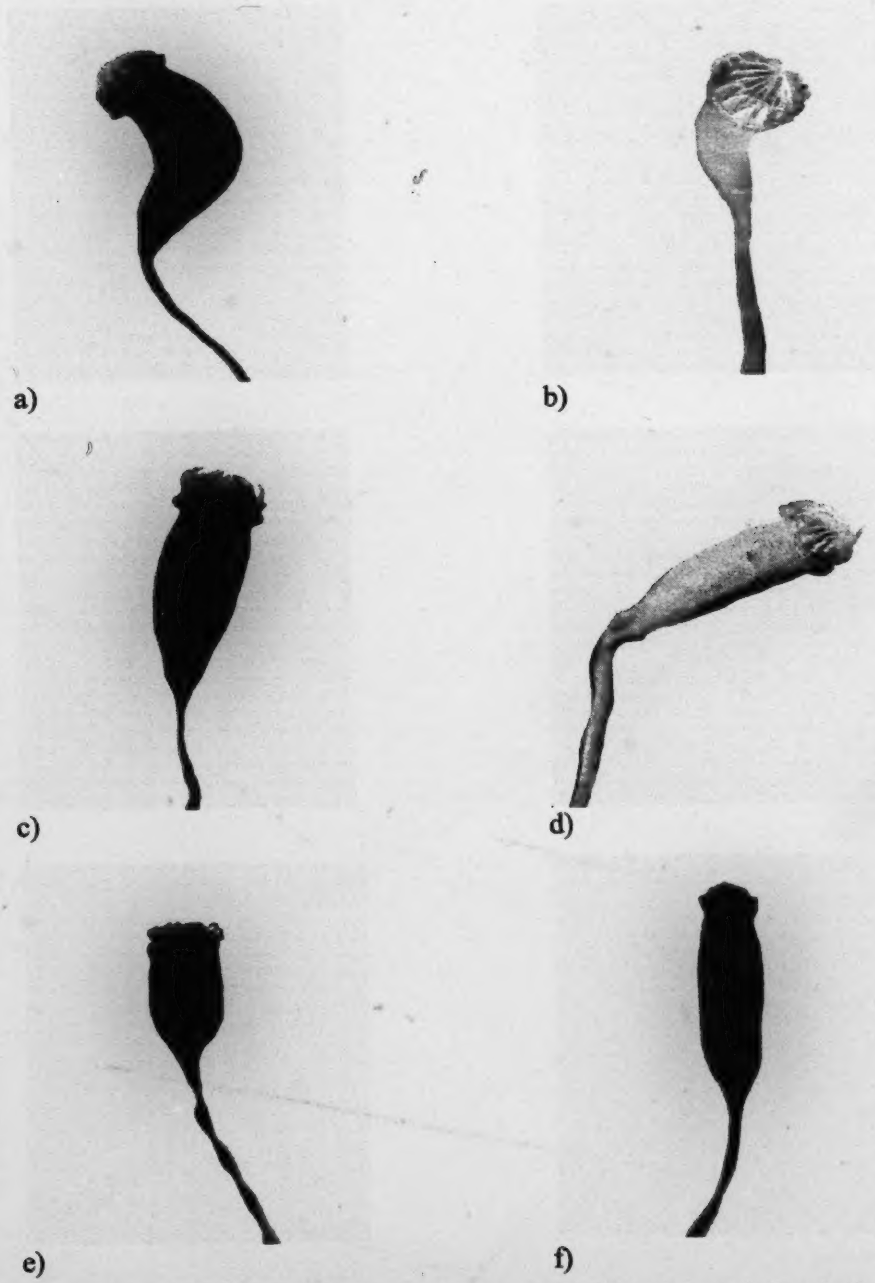

Figure 2.11. Digital images of capsule shape and orientation variation in *Lescuraea*: a),b) asymmetric and arcuate capsules of *L. incurvata* var. *incurvata* (*Krieger & Hebben 1807* ALTA) and *L. patens* (*Krieger & Hebben 1799* ALTA); c),d) asymmetric or symmetric and suberect or inclined capsules of *L. incurvata* var. *incurvata* (*Krieger & Hebben 1807* ALTA) and *L. radicosa* var. *radicosa* (*Krieger & Hebben 1795* ALTA); e),f) symmetric and erect capsules of *L. stenophylla* (*Krieger & Hebben 1801* ALTA) and *L.saxicola* (*Schofield, Iwatsuki & Yoshimura 46206* UBC). Images taken at 250X Mag.

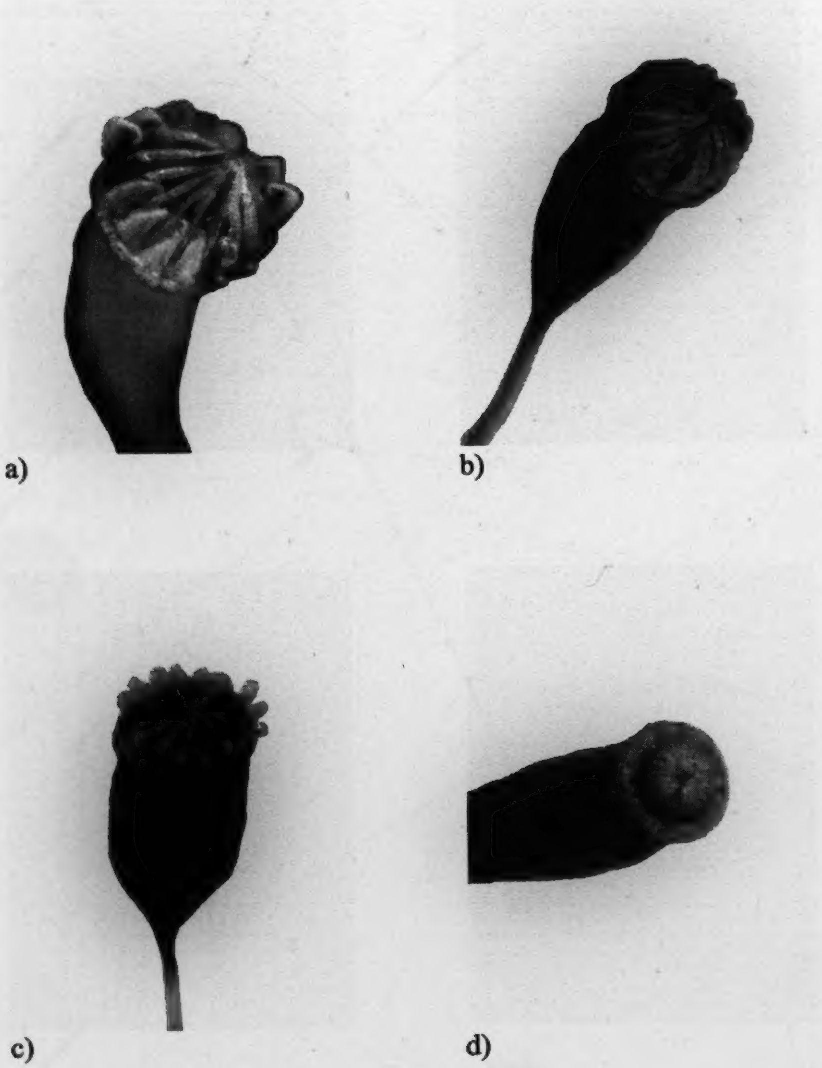

Figure 2.12. Digital images of peristome orientation variation in *Lescuraea*: a),b) exostome incurved and endostome erect in *L. patens* (*Krieger & Hebben 1799* ALTA) and *L. atricha* (*Krieger & Hebben 1859* ALTA); c) exostome recurved below, incurved above and endostome incurved in *L. stenophylla* (*Krieger & Hebben 1801* ALTA); d) exostome erect to somewhat inflexed and endostome erect in *L. saxicola* (*Schofield, Iwatsuki & Yoshimura 46206* UBC). Images taken at 500X Mag.

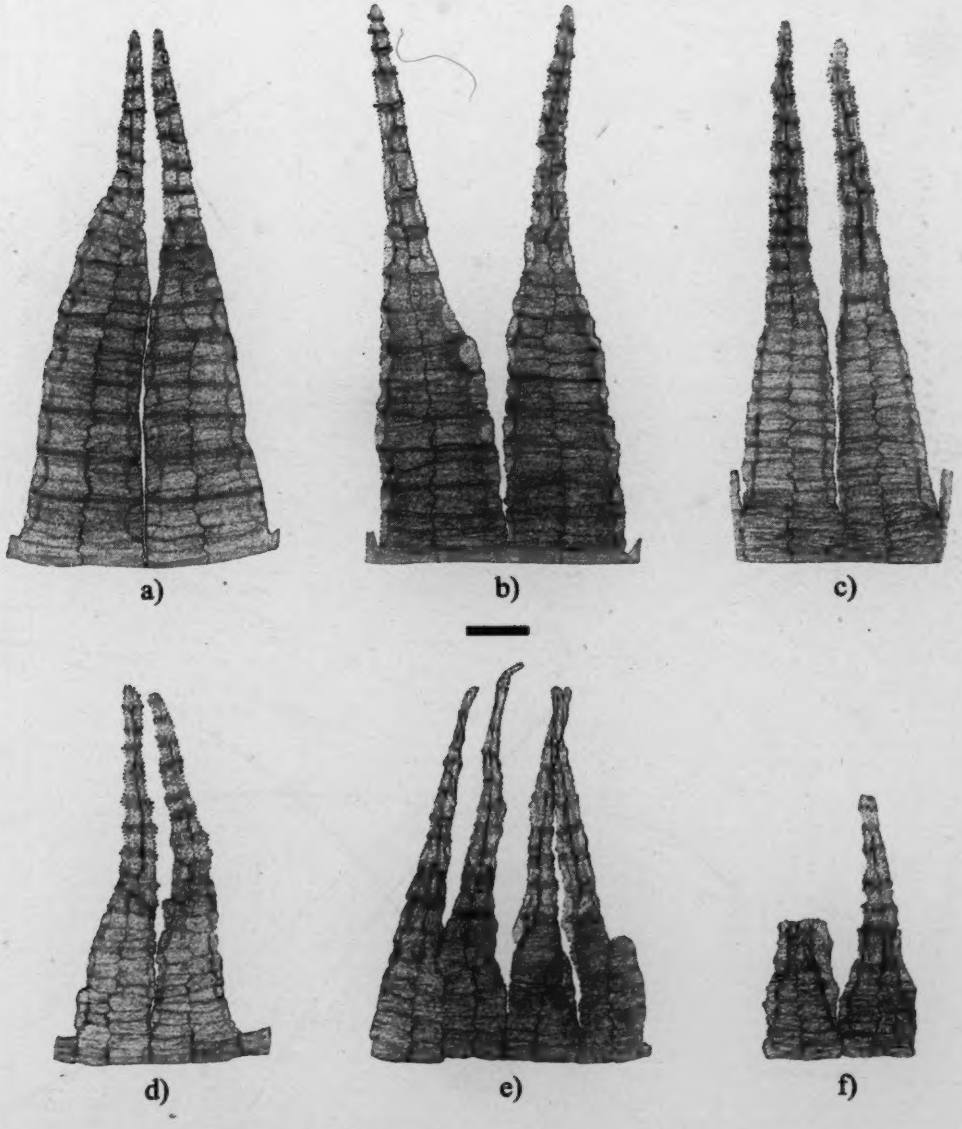

Figure 2.13. Illustrations of exostome variation in *Lescuraea*: a) shouldered teeth with horizontal papillose striae extending nearly 2/3 height of teeth in *L. patens* (*Schofield & Jamieson 83345* UBC); b),c) slightly shouldered teeth with papillose-striae or ridges extending nearly 1/2 height of teeth in *L. radicosa* (*Hermann 20581* WTU) and *L. saviana* (*Baumgartner 1226* CANM); d) unshouldered teeth with papillose-striae or fine ridges extending to 1/3 height of teeth in *L. stenophylla* (*Allen 434* WTU); e),f) unshouldered teeth with ridges extending to 1/3 (or clearly less) height of teeth in *L. saxicola* (*Schofield, Iwatsuki & Yoshimura 46206* UBC, *Ryan* F). Scale bar = 48 µm.

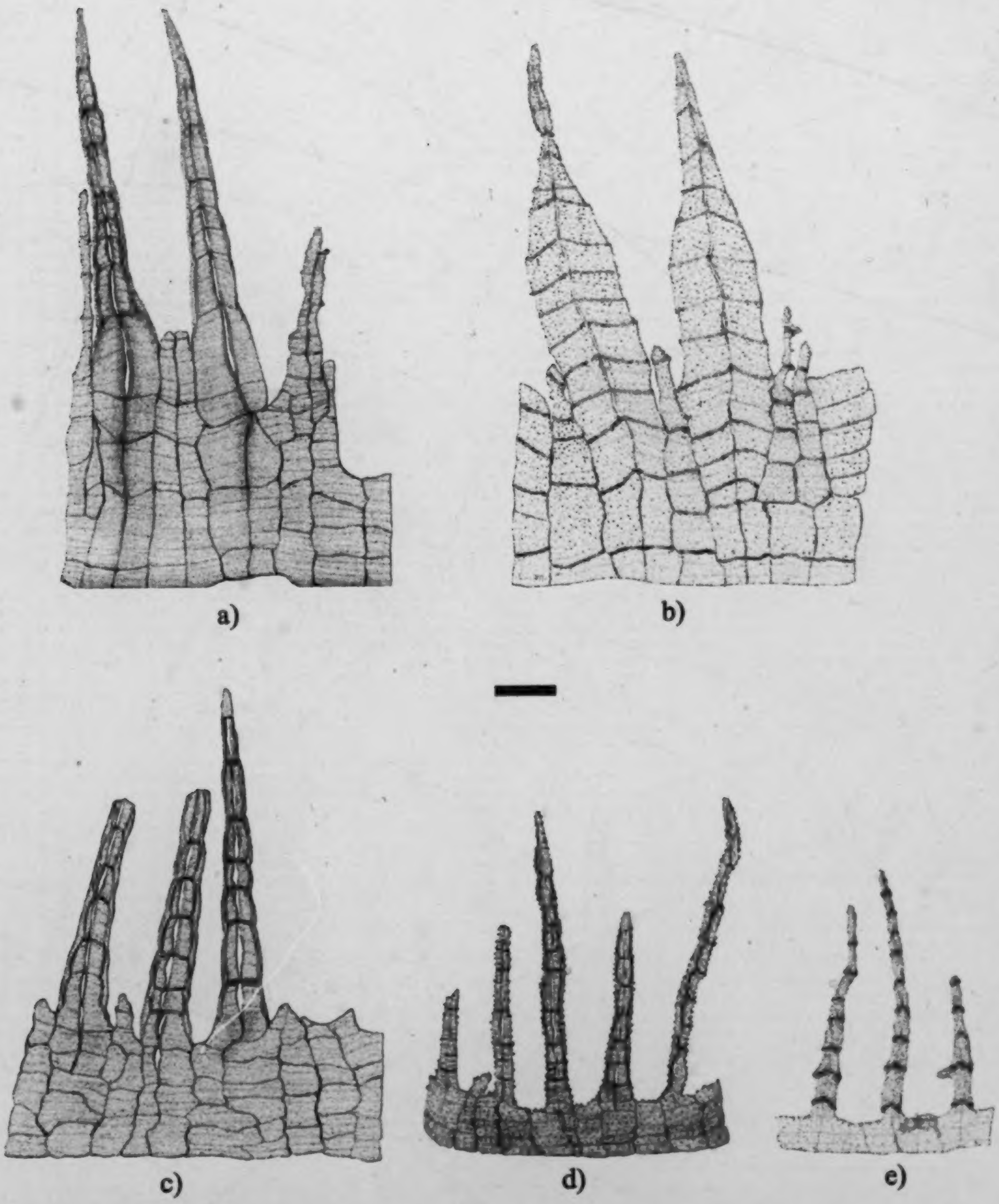

Figure 2.14. Illustrations of endostome variation in *Lescuraea*: a) keeled segments, high basal membrane and filiform cilia in *L. patens* (*Schofield & Jamieson 83345* UBC); b) keeled segments, medium basal membrane and short, broad cilia in *L. radicosa* (*Hermann 20581* WTU); c) narrowly keeled or terete segments, low basal membrane lacking cilia in *L. saviana* (*Baumgartner 1226* CANM); d) terete segments, low basal membrane lacking cilia in *L. stenophylla* (*Allen 24* WTU); e) filiform or peg-like segments, low basal membrane lacking cilia in *L. saxicola* (*Schofield, Iwatsuki & Yoshimura 46206* UBC). Scale bar = 48 µm.

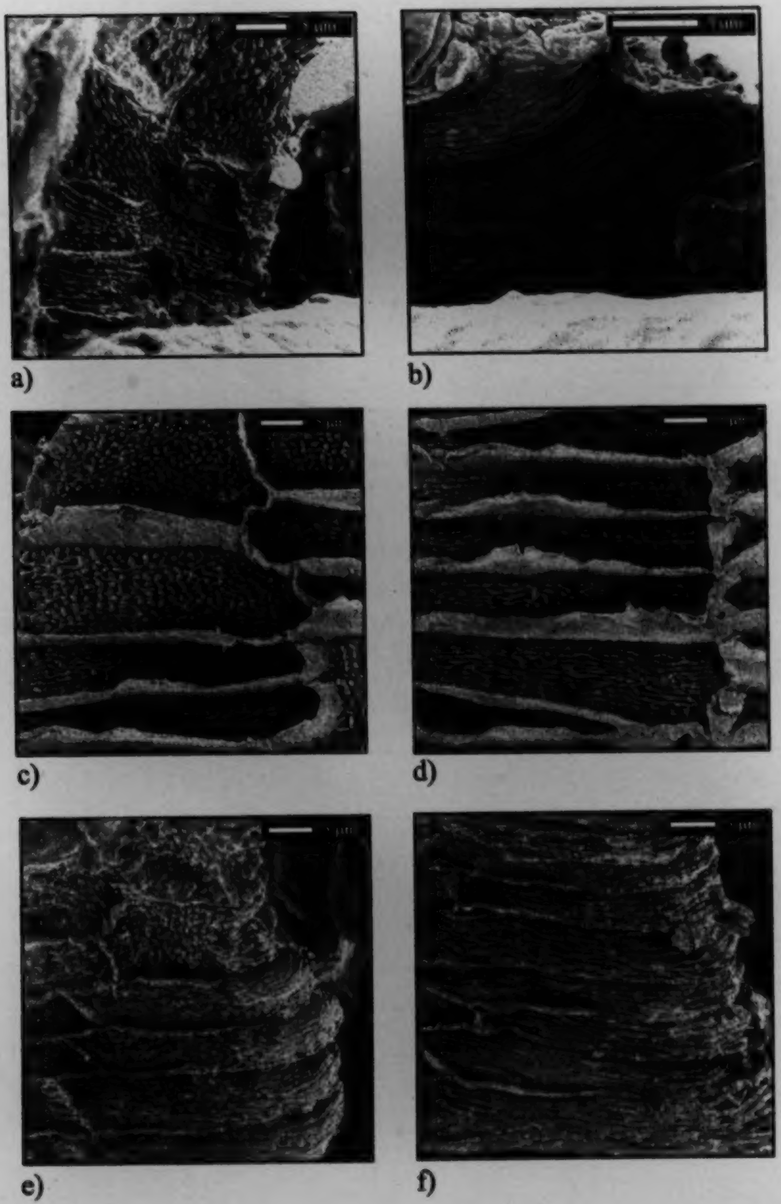

Figure 2.15. Scanning electron micrographs of exostome ornamentation variation in *Lescuraea*: a) mid-tooth showing transition from horizontal ridges (proximal) to papillae (distal) and b) proximal region revealing ridges of *Lescuraea saxicola* (*Ando* UBC); c) mid-tooth showing transition from undulating horizontal papillose-striae to papillae and d) proximal region revealing undulating horizontal papillose-striae of *L. incurvata* (*Schofield 56823* UBC); e) mid-tooth showing transition from undulating horizontal papillose-striae to papillae and f) proximal region revealing horizontal striae of *L. saviana* (*Glowacki 25181/17930* Syntype-GJO).

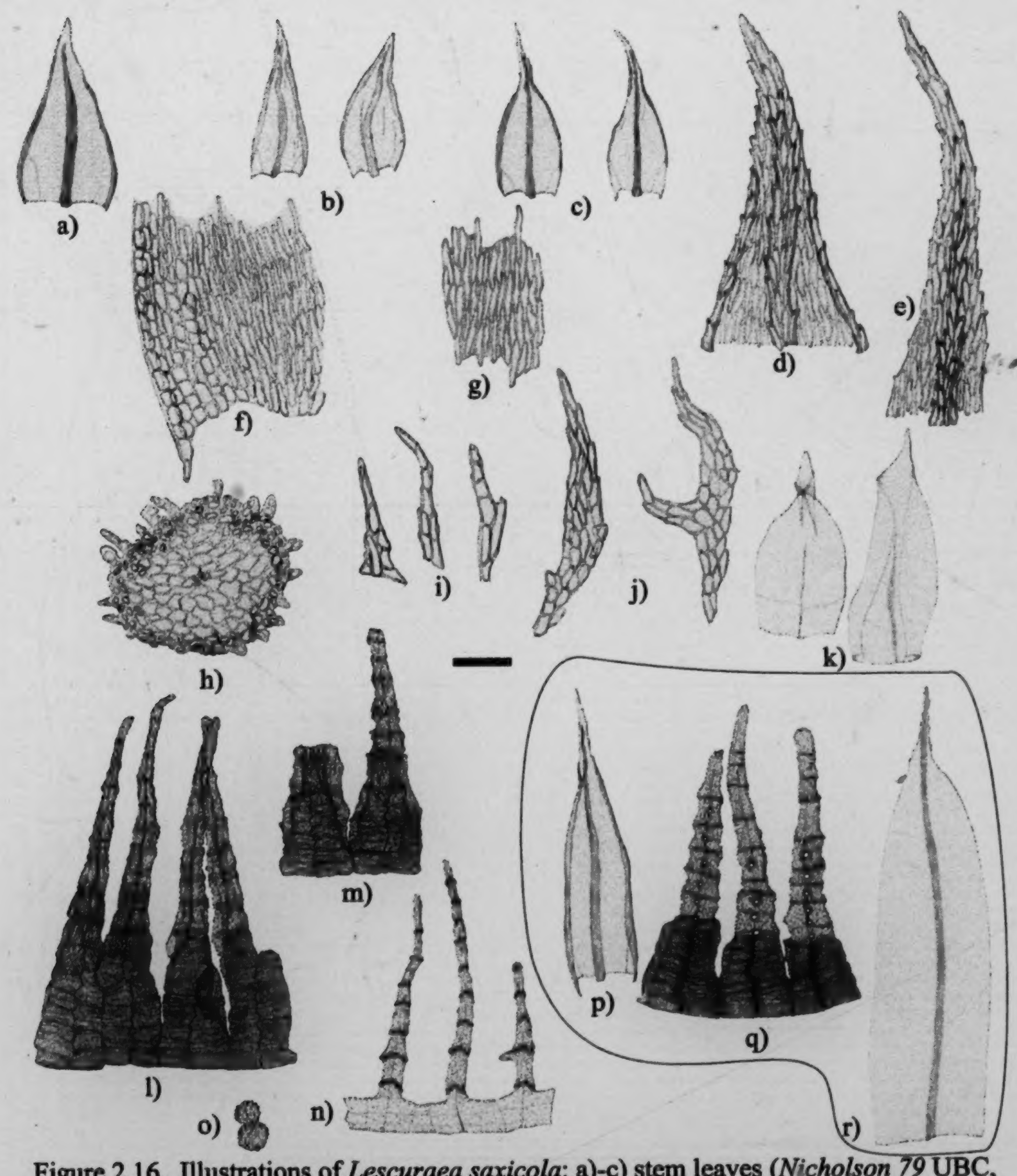

Figure 2.16. Illustrations of *Lescuraea saxicola*: a)-c) stem leaves (*Nicholson 79* UBC, *Stormer* UBC, *Ireland & Bellilio-Trucco 18679* F); d),e) stem leaf apices (*Ireland & Bellilio-Trucco 18679* F, *Iwatsuki 1011* UBC); f),g) alar and basal, and median cells (*Ireland & Bellilio-Trucco 18679* F); h) stem transverse section (*Tan & Keng 78-484* UBC); i),j) paraphyllia (*Belland 4177* UBC); k) inner perichaetial leaves (*Iwatsuki 1011* UBC); l),m) exostomes (*Schofield, Iwatsuki & Yoshimura 46206* UBC, *Ryan* F); n) endostome (*Schofield, Iwatsuki & Yoshimura 46206* UBC); o) spores (*Schofield, Iwatsuki & Yoshimura 46206* UBC). *L. mutabilis*: p)-r) stem leaf, exostome, inner perichaetial leaf (*Mougeot & Stirpes* UBC). Scale bar = 316 μm for a)-c),k),p),r); 48 μm for d)-j),l)-o),q).

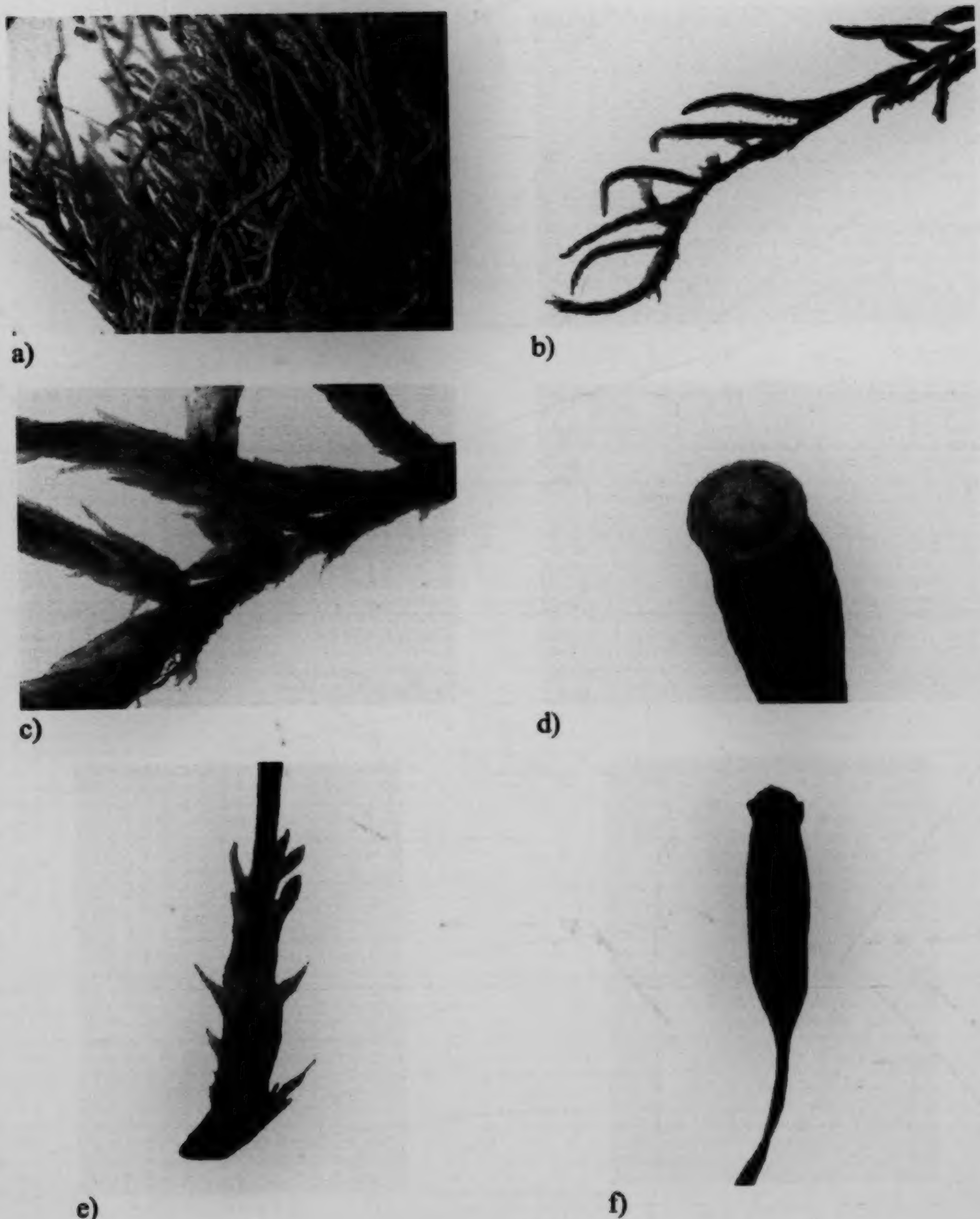

Figure 2.17. Digital images of *Lescuraea saxicola*: a) habit; b) stem; c) portion of stem; d) peristome; e) perichaetial stance; f) capsule. Specimens a)-c), e) (*Berggren 162* US); d),f) (*Schofield, Iwatsuki & Yoshimura 46206* UBC). Images taken at: 60X (a); 120X (b); 250X (d); 500X Mag. (c,e,f).

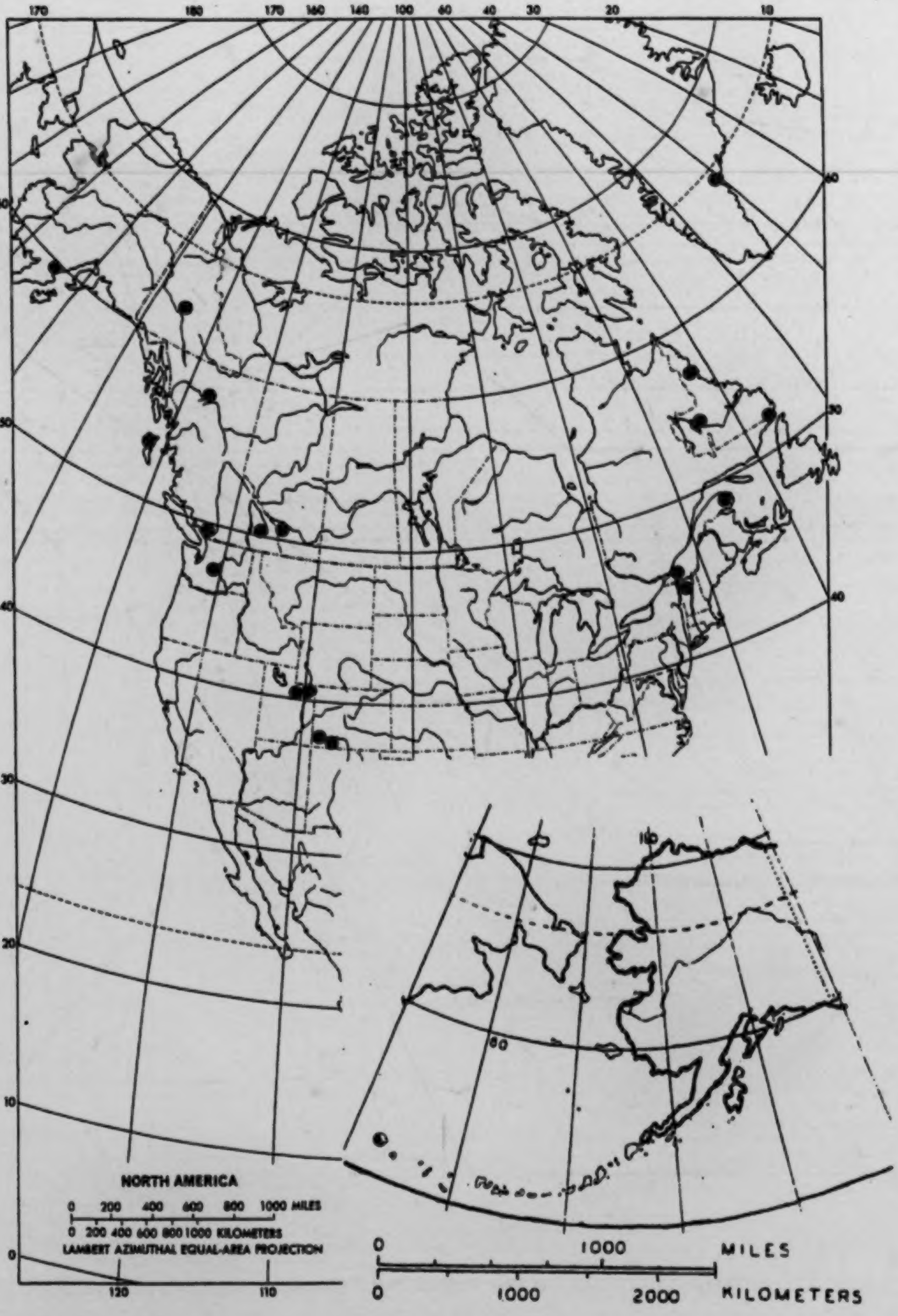
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Figure 2.18. Distribution of *Lescuraea saxicola*

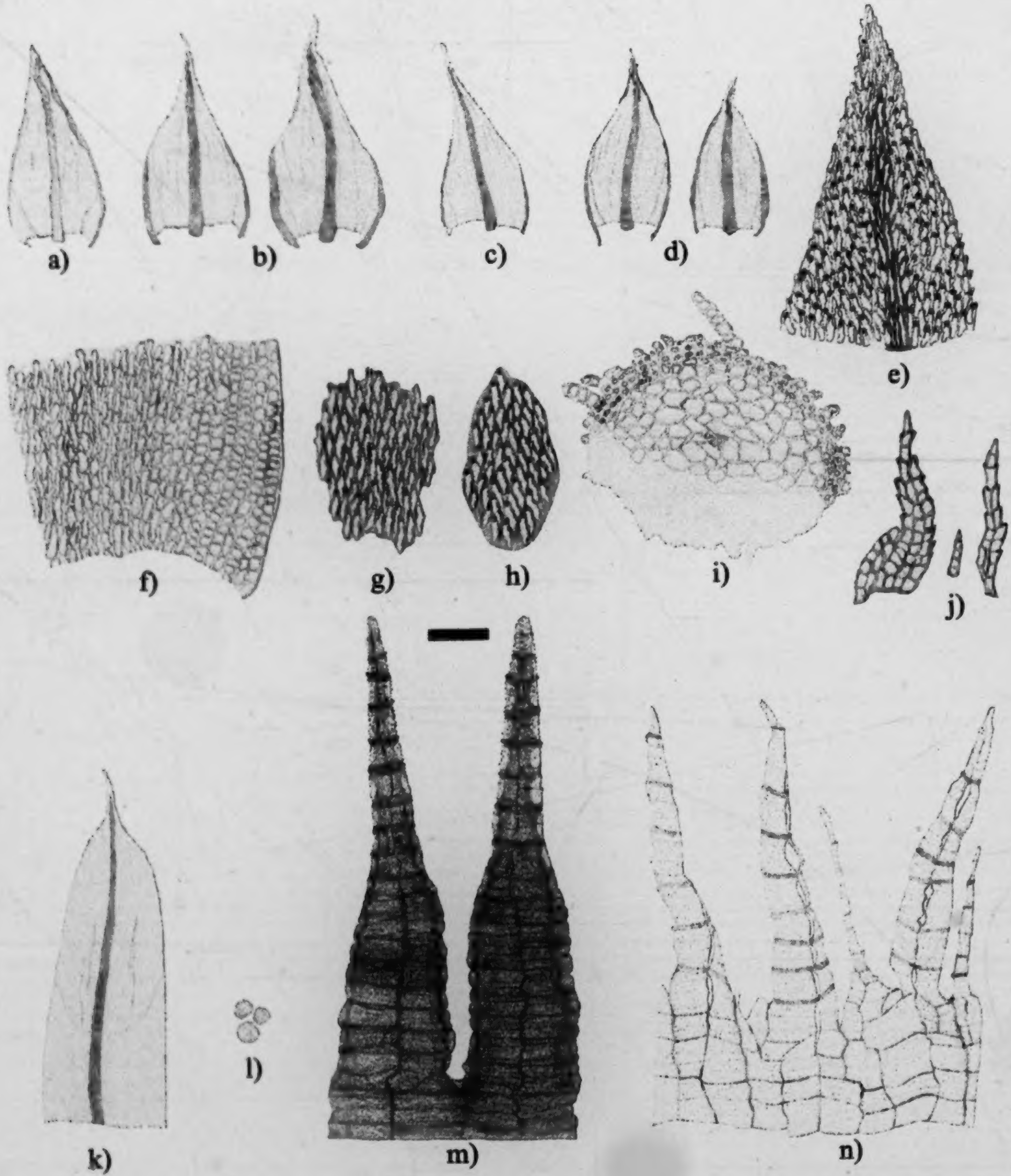

Figure 2.19. Illustrations of *Lescuraea atricha*: a)-d) stem leaves (*Van Velzen & Leong 302.8069* UBC, *Lawton 4994* WTU, *Vanderspek & Ralph 60-1030B* WTU, *Lawton 4553* WTU); e) stem leaf apex (*Van Velzen & Leong 302.8069* UBC); f)-h) alar and basal, median, and distal cells (*Van Velzen & Leong 302.8069* UBC); i) stem transverse section (*Macoun 332* S); j) paraphyllia (*Macoun 332* S); k)-n) inner perichaetial leaf, spores, exostome, and endostome (*Frye 546* WTU). Scale bar = 316 µm for a)-d),k); 48 µm for e)-j),l)-n).

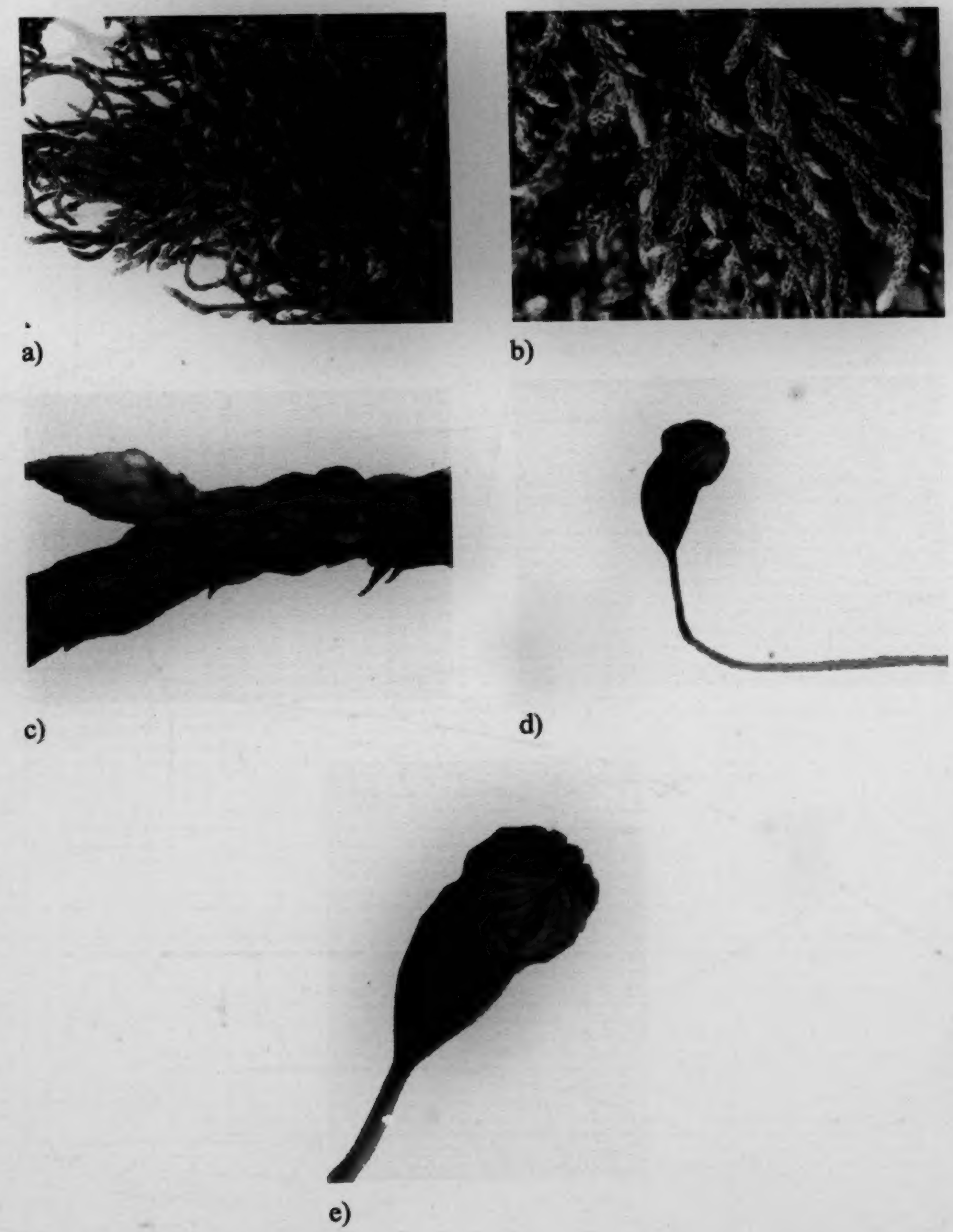

Figure 2.20. Digital images of *Lescuraea atricha*: a) habit; b) stems; c) portion of stem; d),e) capsule. All images from *Krieger & Hebben 1859* ALTA. Images taken at: 60X (a); 120X (b); 500X (c,e); 250X Mag.(d).

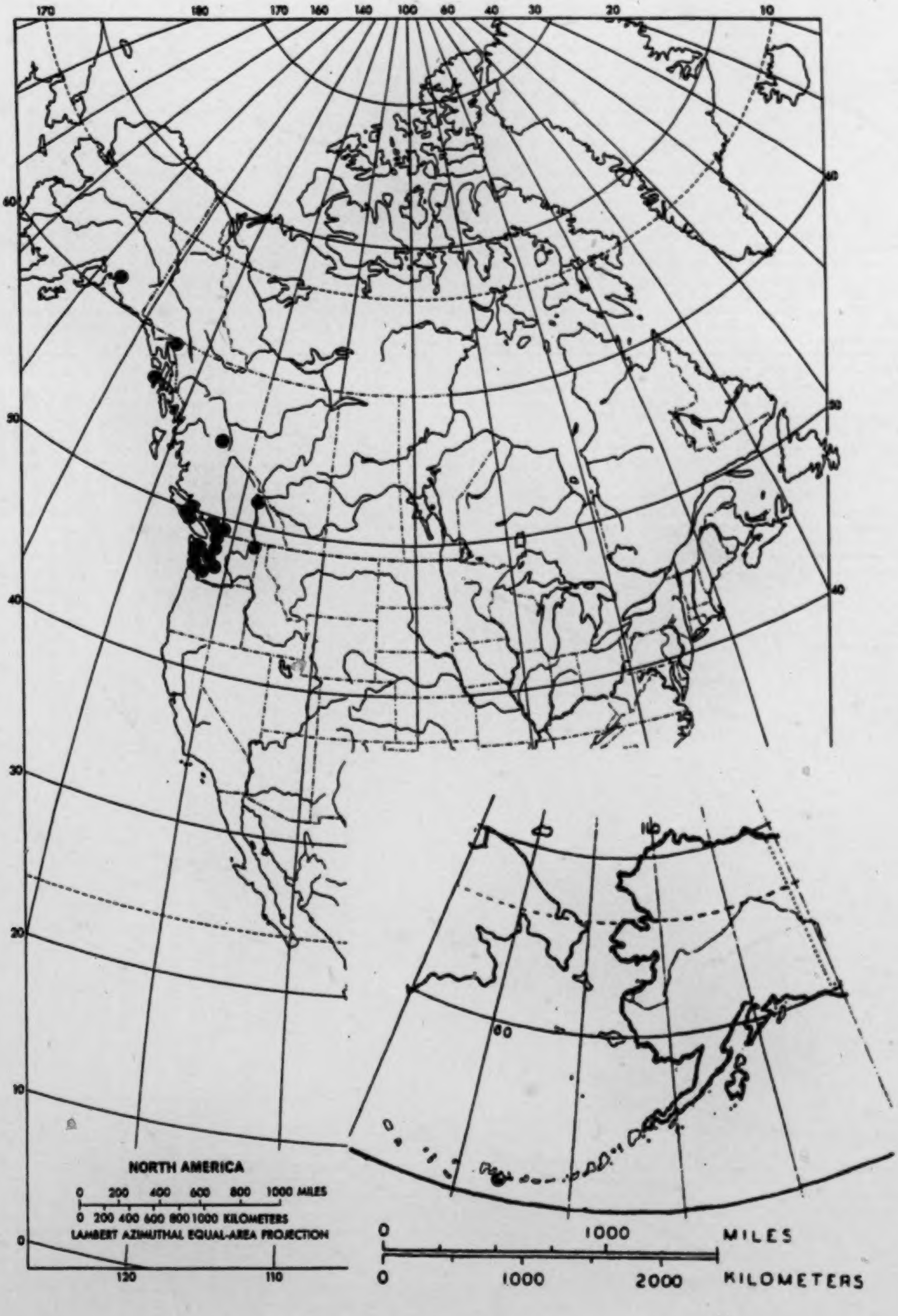
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Figure 2.21. Distribution of *Lescuraea atricha*

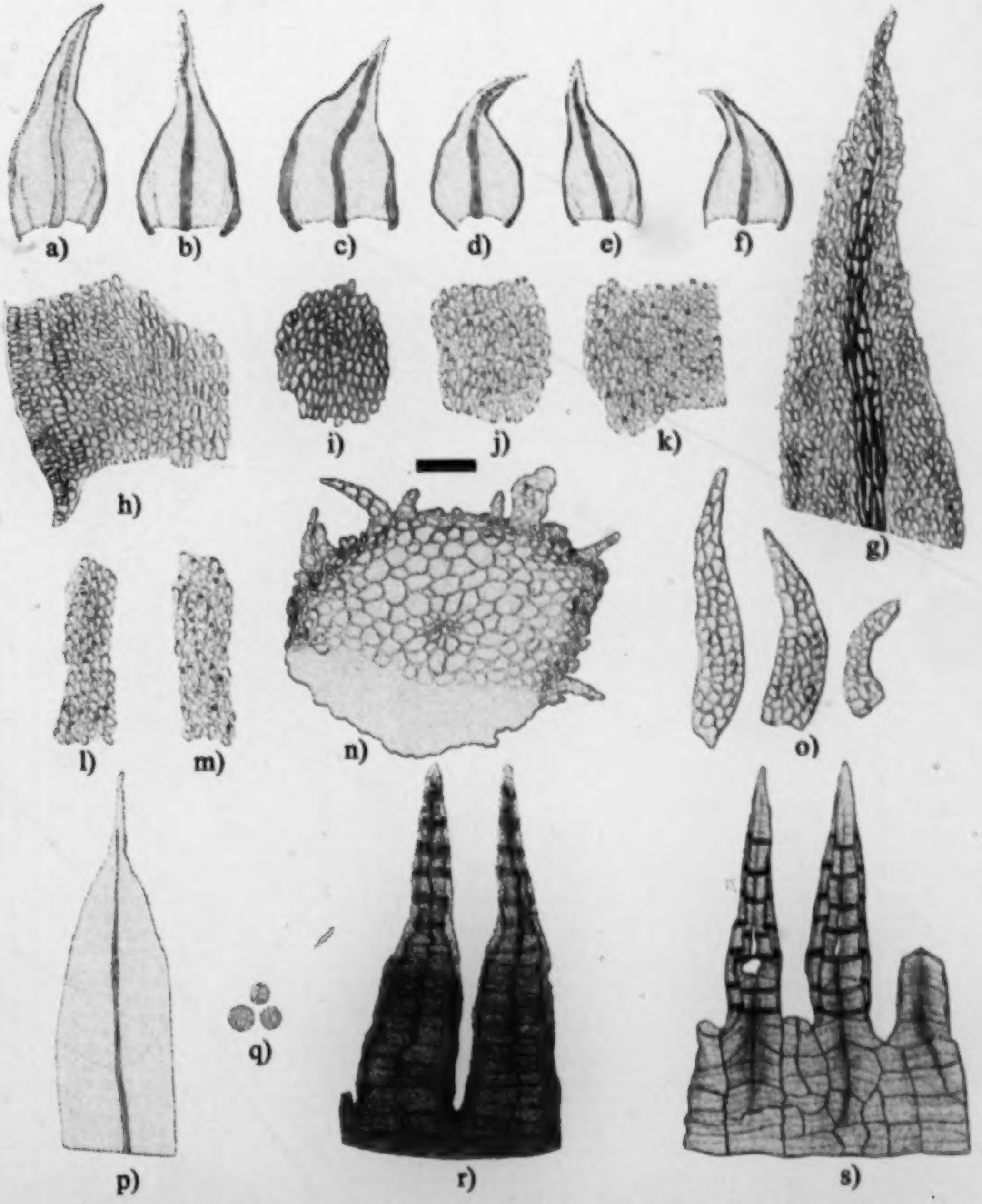

Figure 2.22. Illustrations of *Lescuraea incurvata* var. *incurvata*: a)-f) stem leaves (*Ireland 6618* US, *Ireland 6469* FH, *Ochyra 59* UC/JEPS, *Welch 15299* NY, *Schofield 108719* NY); g) stem apex (*Ireland 6618* US); h) alar and basal cells (*Ireland 6469* FH); i)-k) median cells (*Ireland 6469* FH, *Ireland 6618* US, *Welch 15299* NY); l),m) distal cells (*Ireland 6618* US, *Welch 15299* NY); n) stem transverse section (*Buck 30362* NY); o) paraphyllia (*Buck 30362* NY); p) inner perichaetial leaf (*Ludwig* LECTOTYPE G); q) spores (*Buck 30362* NY); r),s) exostome and endostome (*Ludgwig* LECTOTYPE G). Scale bar = 316 µm for a)-f),p); 48 µm for g)-o),q)-s).

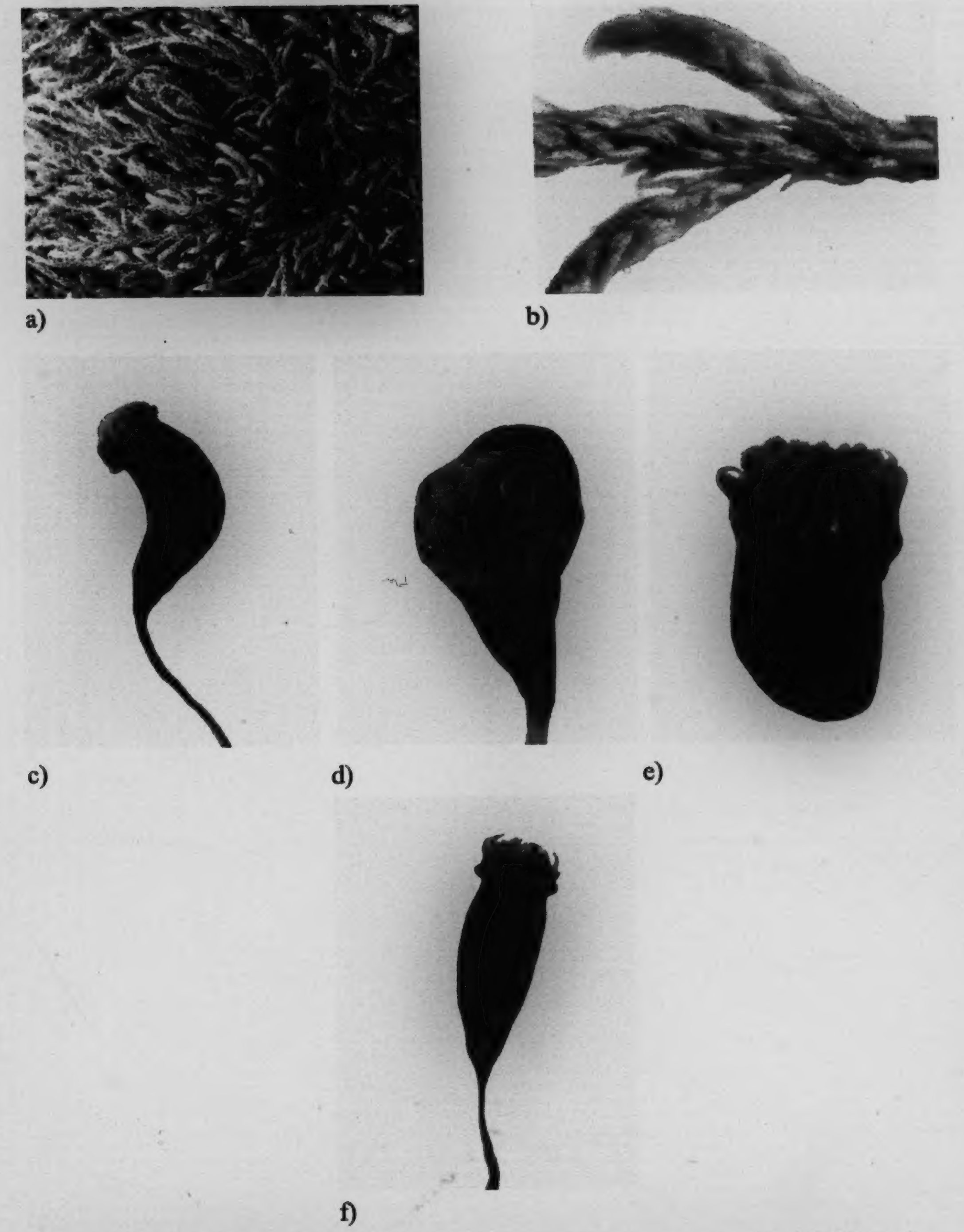

Figure 2.25. Digital images of *Lescuraea incurvata* var. *incurvata*: a) habit; b) portion of stem; c) zygomorphic capsule; d) peristome; e) endostome revealed; f) suberect capsule. All images from *Krieger & Hebben 1807* ALTA. Images taken at 60X (a); 250X (c,f); 500X Mag.(d,e).

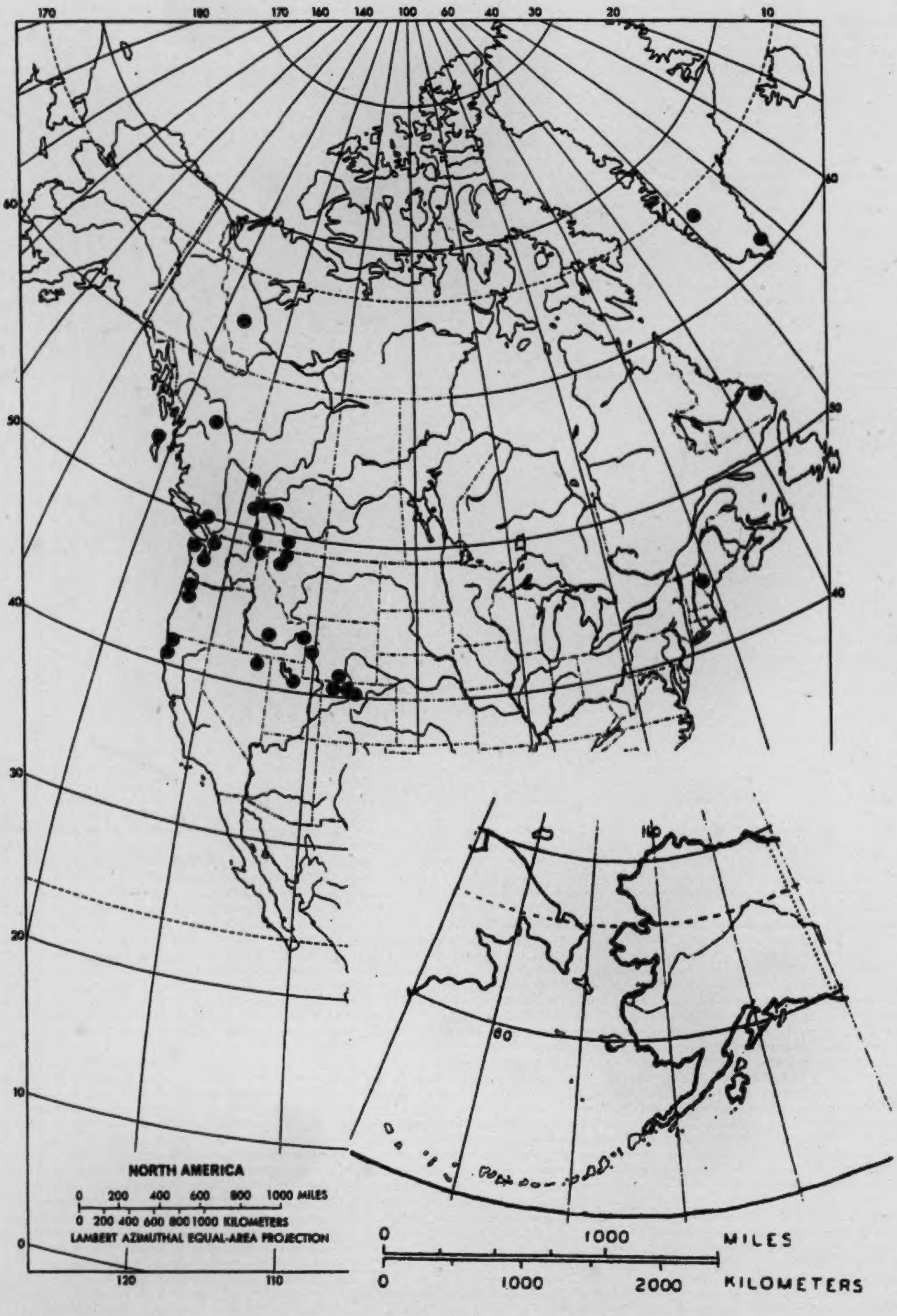
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Figure 2.26. Distribution of *Lescuraea incurvata* var. *incurvata*

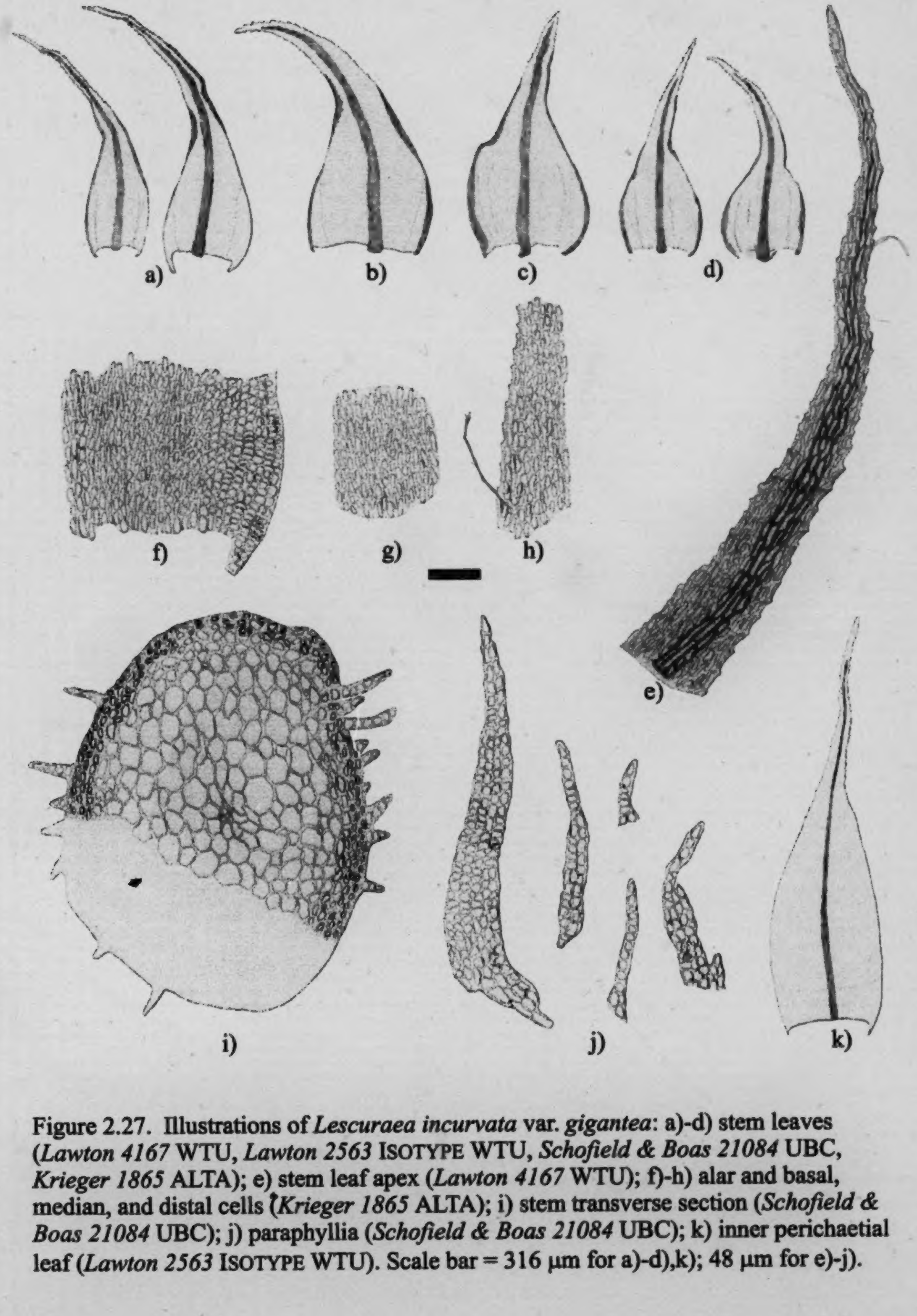

Figure 2.27. Illustrations of *Lescuraea incurvata* var. *gigantea*: a)-d) stem leaves (*Lawton 4167* WTU, *Lawton 2563* ISOTYPE WTU, *Schofield & Boas 21084* UBC, *Krieger 1865* ALTA); e) stem leaf apex (*Lawton 4167* WTU); f)-h) alar and basal, median, and distal cells (*Krieger 1865* ALTA); i) stem transverse section (*Schofield & Boas 21084* UBC); j) paraphyllia (*Schofield & Boas 21084* UBC); k) inner perichaetial leaf (*Lawton 2563* ISOTYPE WTU). Scale bar = 316 μm for a)-d),k); 48 μm for e)-j).

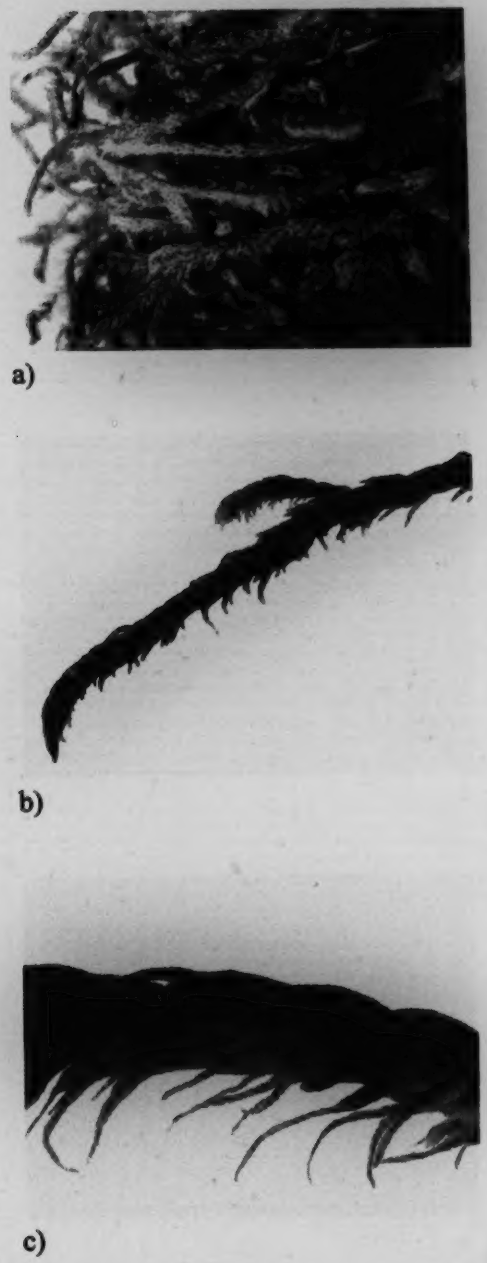

Figure 2.28. Digital images of *Lescuraea incurvata* var. *gigantea*: a) habit; b) stem; c) portion of stem. All images from *Krieger & Hebben 1867* ALTA. Images taken at 60X (a), 120X (b), 500X Mag. (c).

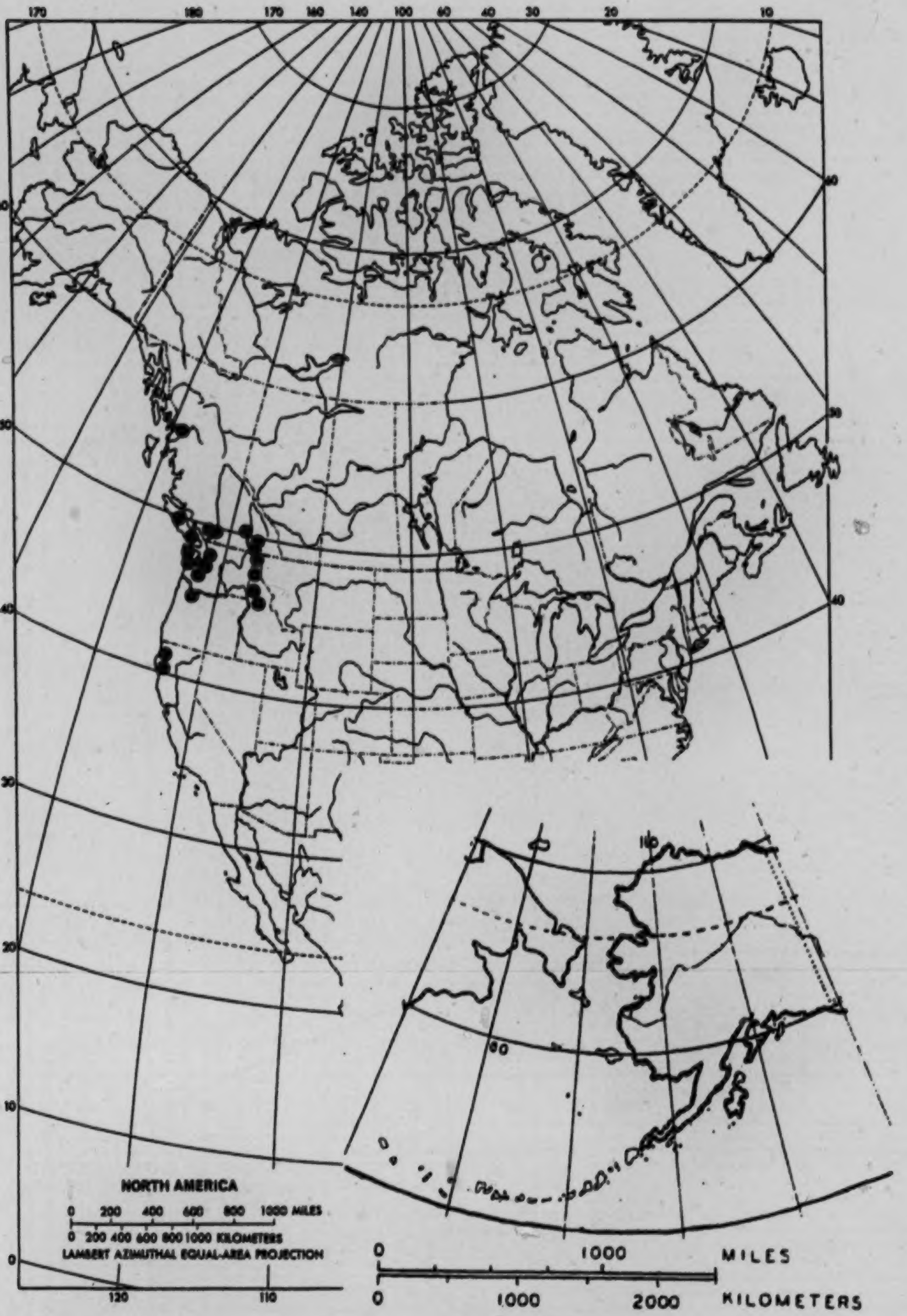
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Figure 2.29. Distribution of *Lescuraea incurvata* var. *gigantea*

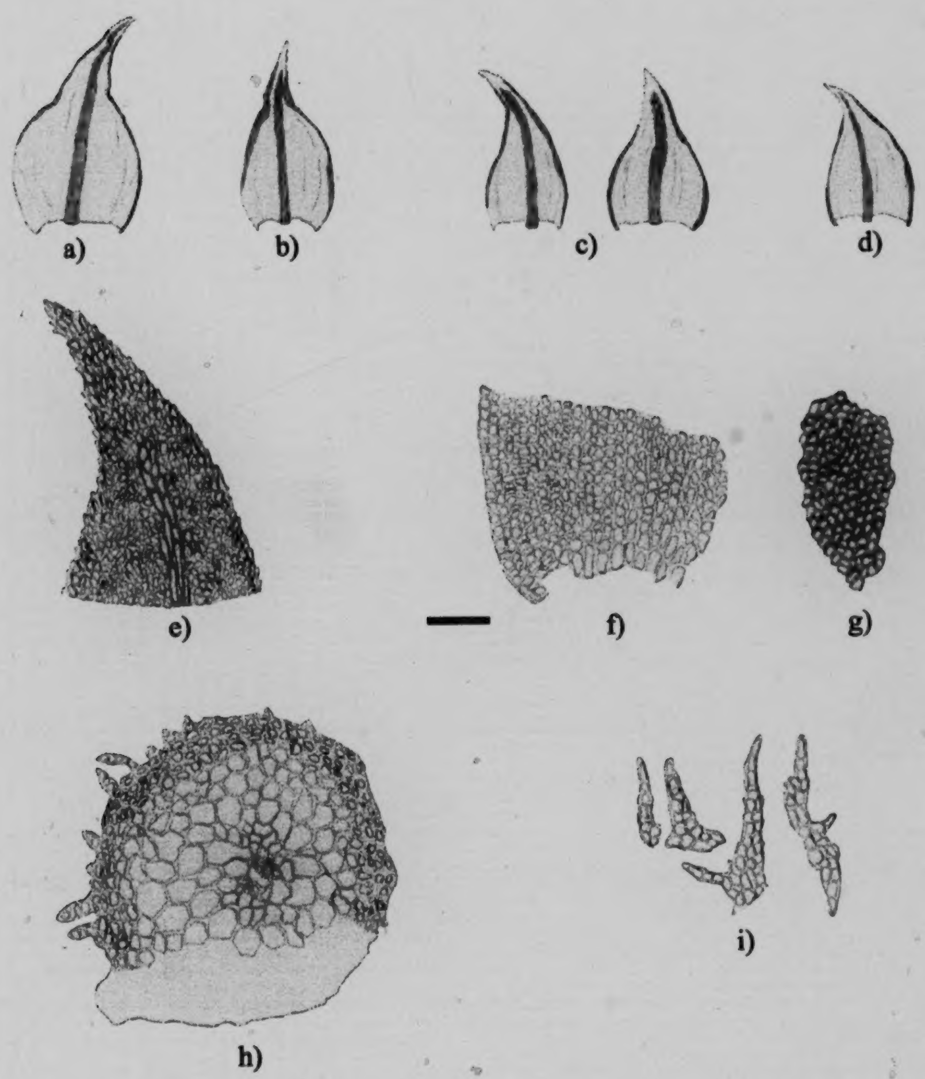

Figure 2.30. Illustrations of *Lescuraea incurvata* var. *tenuiretis*: a)-d) stem leaves (*Culmann* LECTOTYPE Z, *McCune 47200* OSC/ORE, *Bird & Glenn 12962* CANM, *Bird & Lakusta 14972* CANM); e) stem leaf apex (*McCune 4720* OSC/ORE); f),g) alar and basal, and median cells (*McCune 47200* OSC/ORE); h) stem transverse section (*Flowers 1642* COLO);i) paraphyllia (*McCune 4720* OSC/ORE).
Scale bar = 316 μm for a)-d); 48 μm for e)-i).

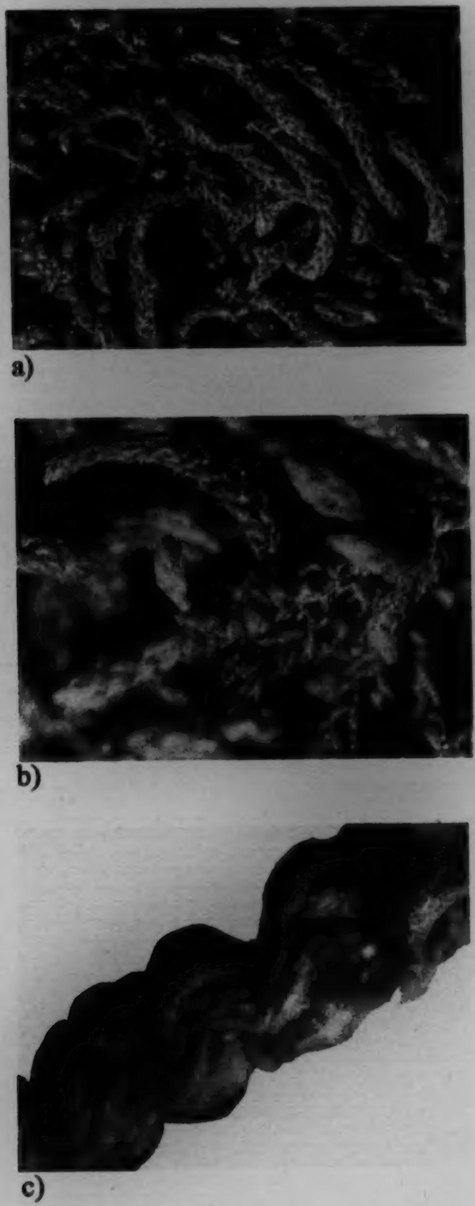

Figure 2.31. Digital images of *Lescuraea incurvata* var. *tenuiretis*: a) habit; b) stem; c) portion of stem. All images from *Krieger & Hebben 1801* ALTA. Images taken at 60X (a), 120X (b), 500X Mag. (c).

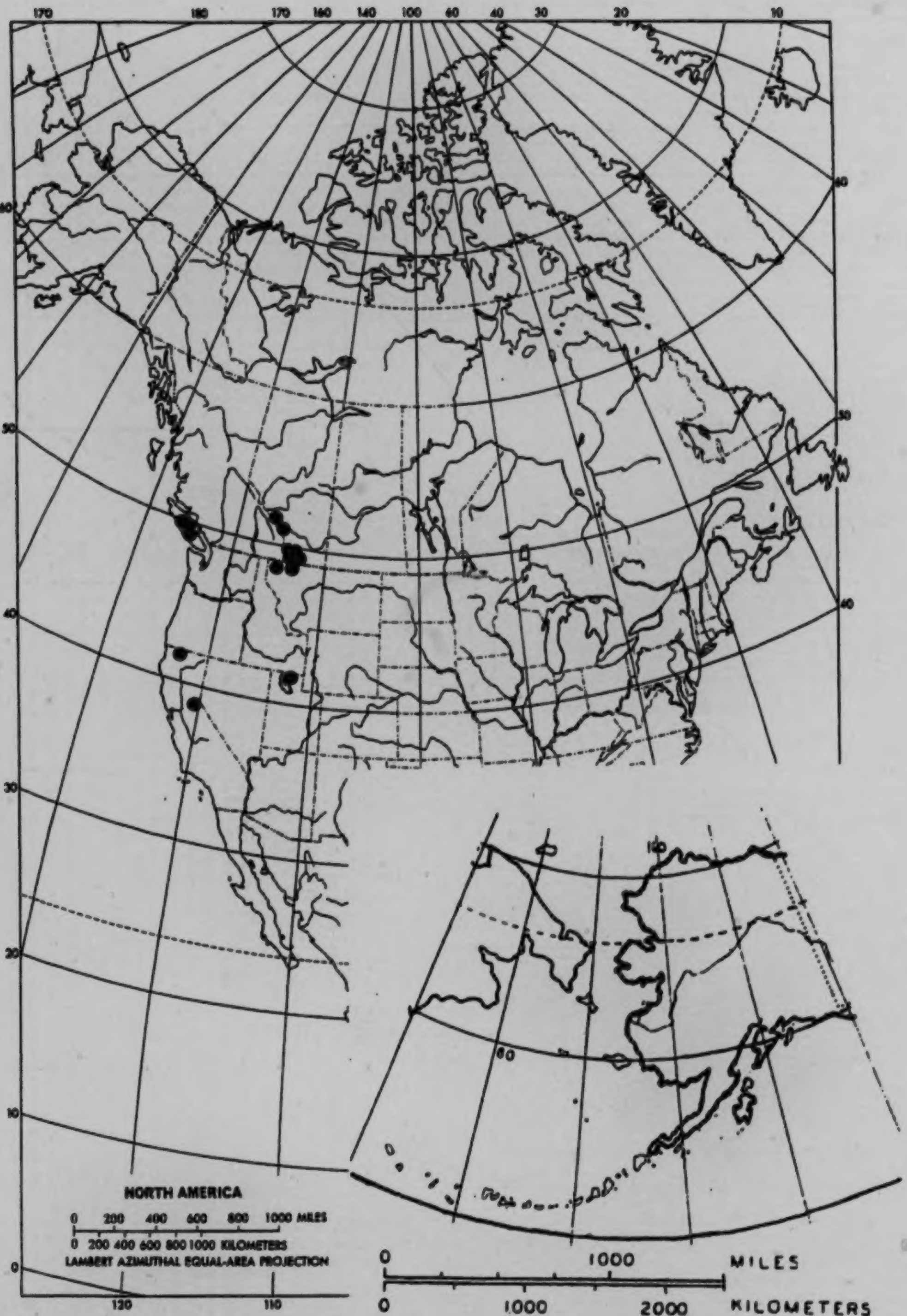
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Figure 2.32. Distribution of *Lescuraea incurvata* var. *tenuiretis*

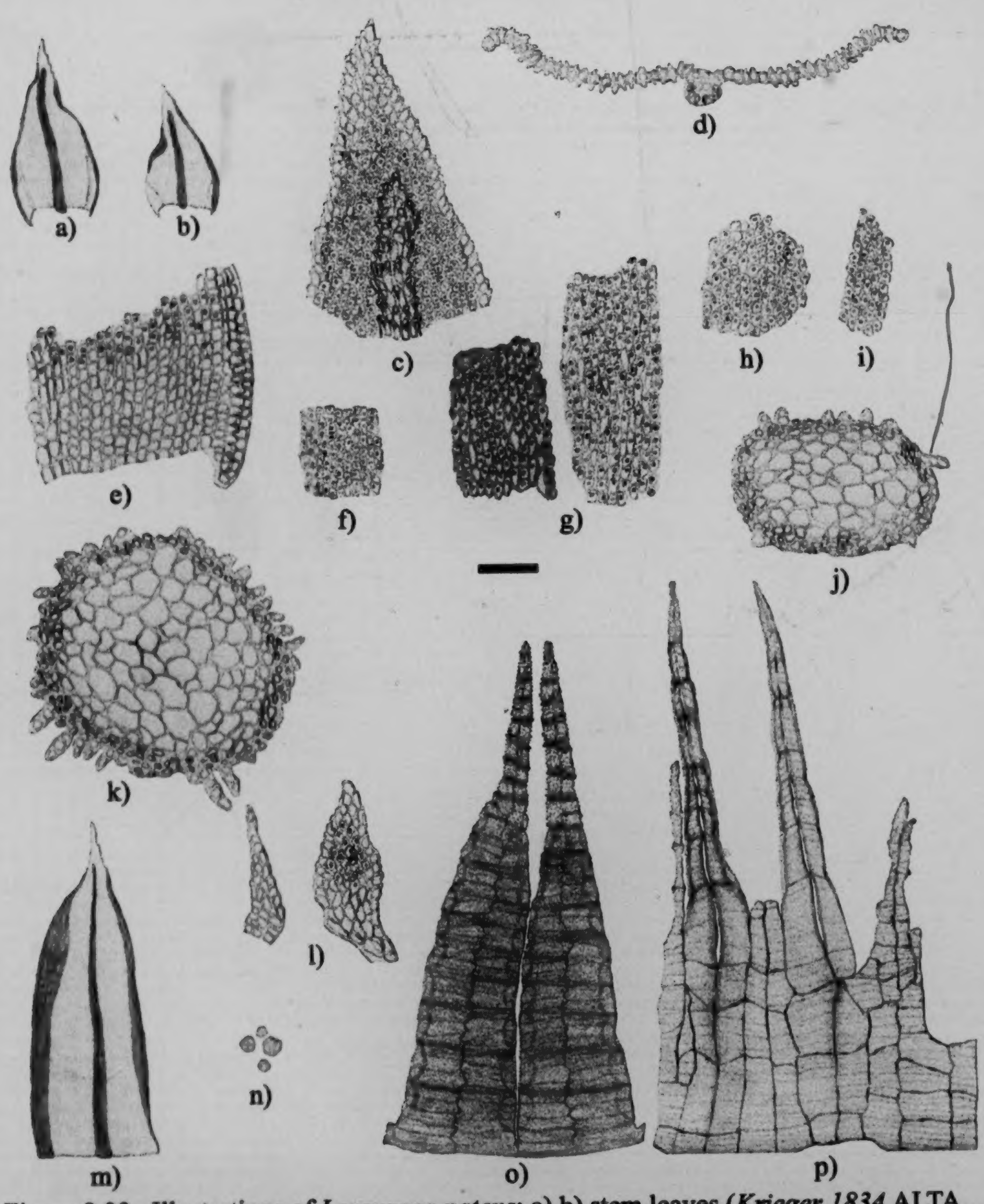

Figure 2.33. Illustrations of *Lescuraea patens*: a),b) stem leaves (*Krieger 1834* ALTA, *MacFadden* COLO); c) stem leaf apex (*Lawton 4832* UC/JEPS); d) stem leaf transverse section (*Belland, Schofield & Weber 10666* UBC); e) alar and basal cells (*Krieger 1834* ALTA); f),g) median cells (*MacFadden* COLO, *Krieger 1834* ALTA); h),i) distal cells (*Krieger 1834* ALTA, *MacFadden* COLO); j),k) stem transverse sections (*Schofield 104547* UBC, *Belland, Schofield &Weber 10666* UBC); l) paraphyllia (*Krieger 1834* ALTA); m) inner perichaetial leaf (*Lawton 4832* UC/JEPS); n),o),p) spores, exostome, and endostome (*Schofield & Jamieson 83345* UBC). Scale bar = 316 µm for a),b),m); 48 µm for c)-l),n)-o).

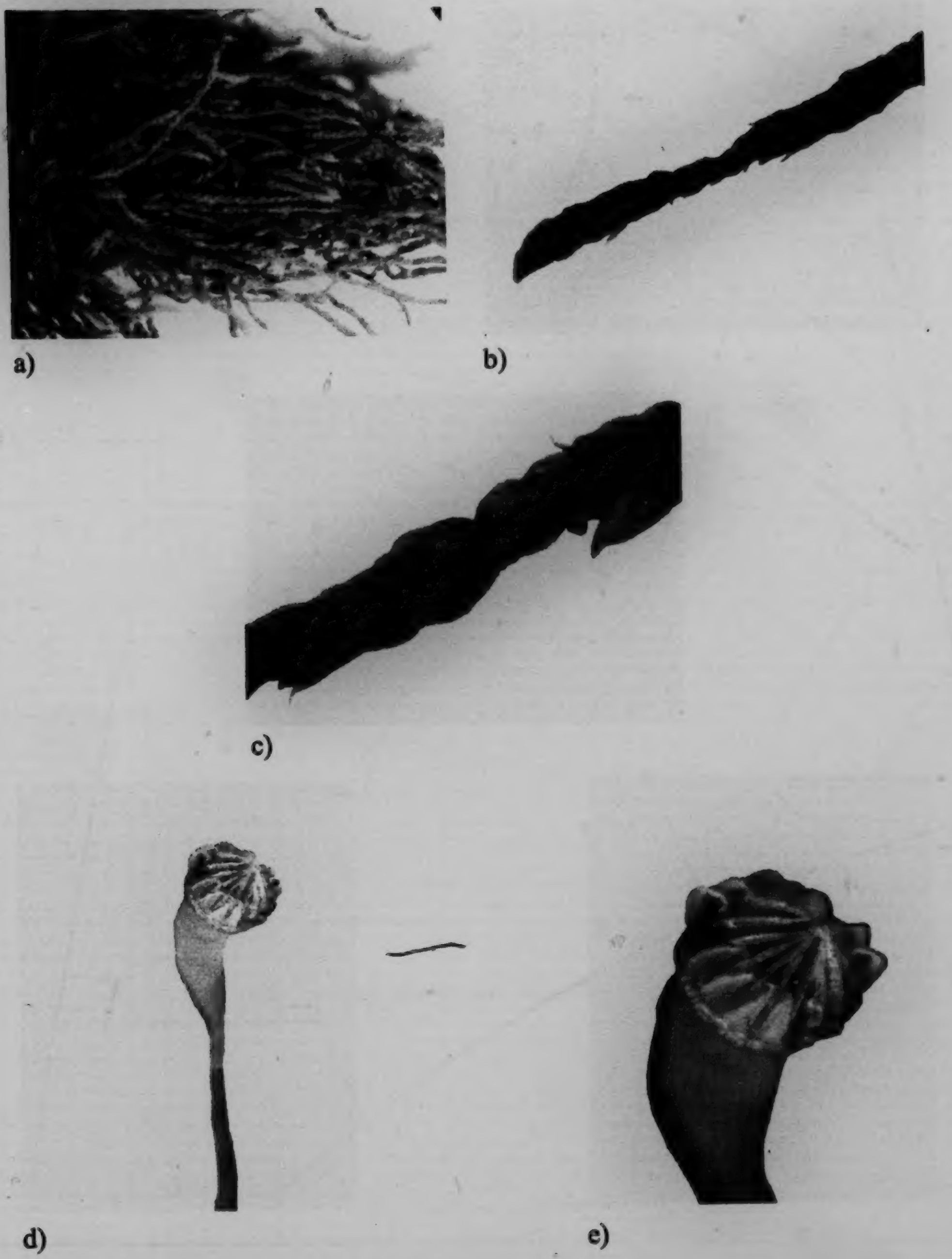

Figure 2.34. Digital Images of *Lescuraea patens*: a) habit; b) stem; c) portion of stem; d) sporophyte, e) capsule revealing peristome. Images a)-c) from *Krieger & Hebben 1834* ALTA; d),e) from *Krieger & Hebben 1799* ALTA. Images taken at 60X (a), 250X (b,d), 500X (c,e).

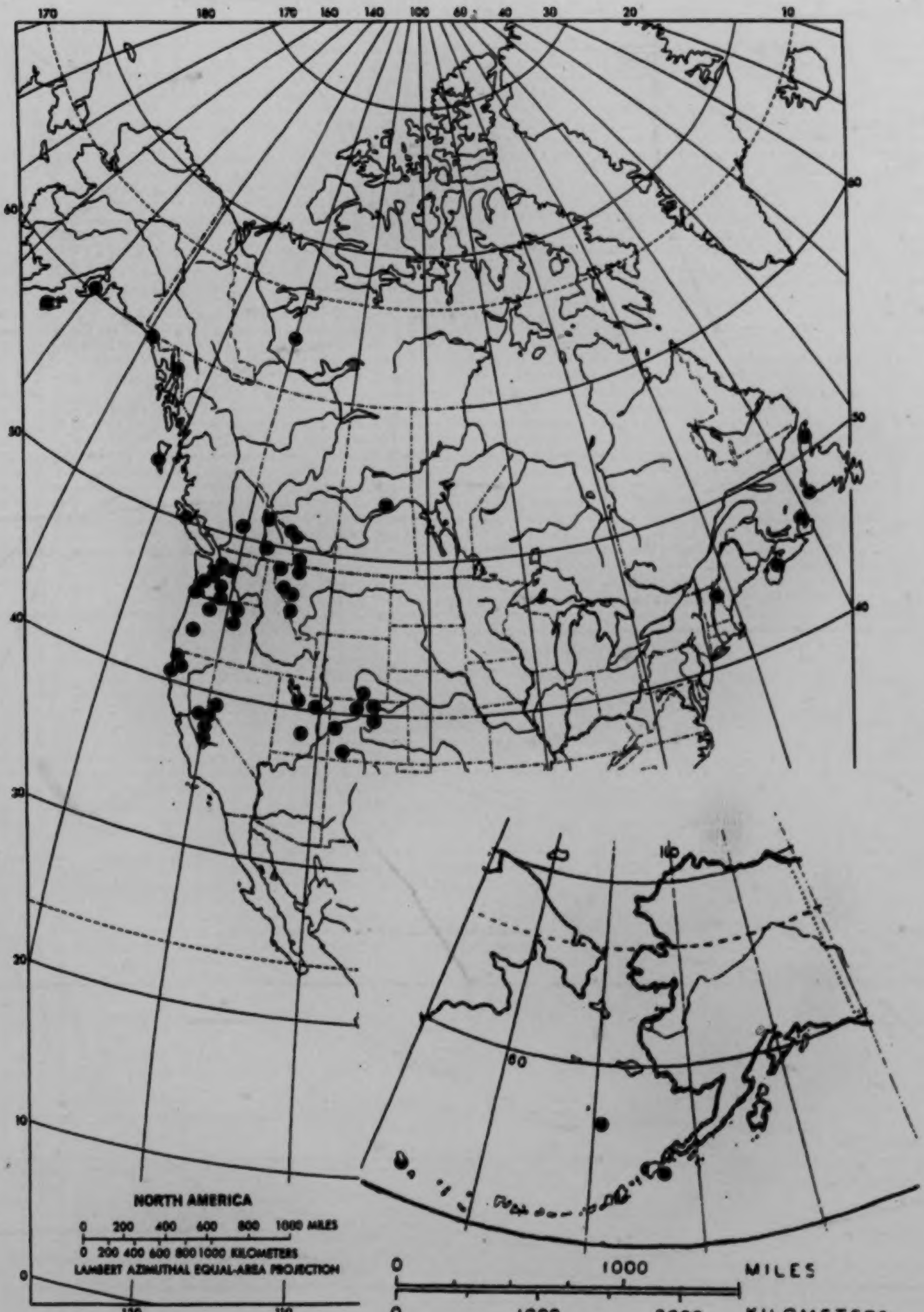
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Figure 2.35. Distribution of *Lescuraea patens*

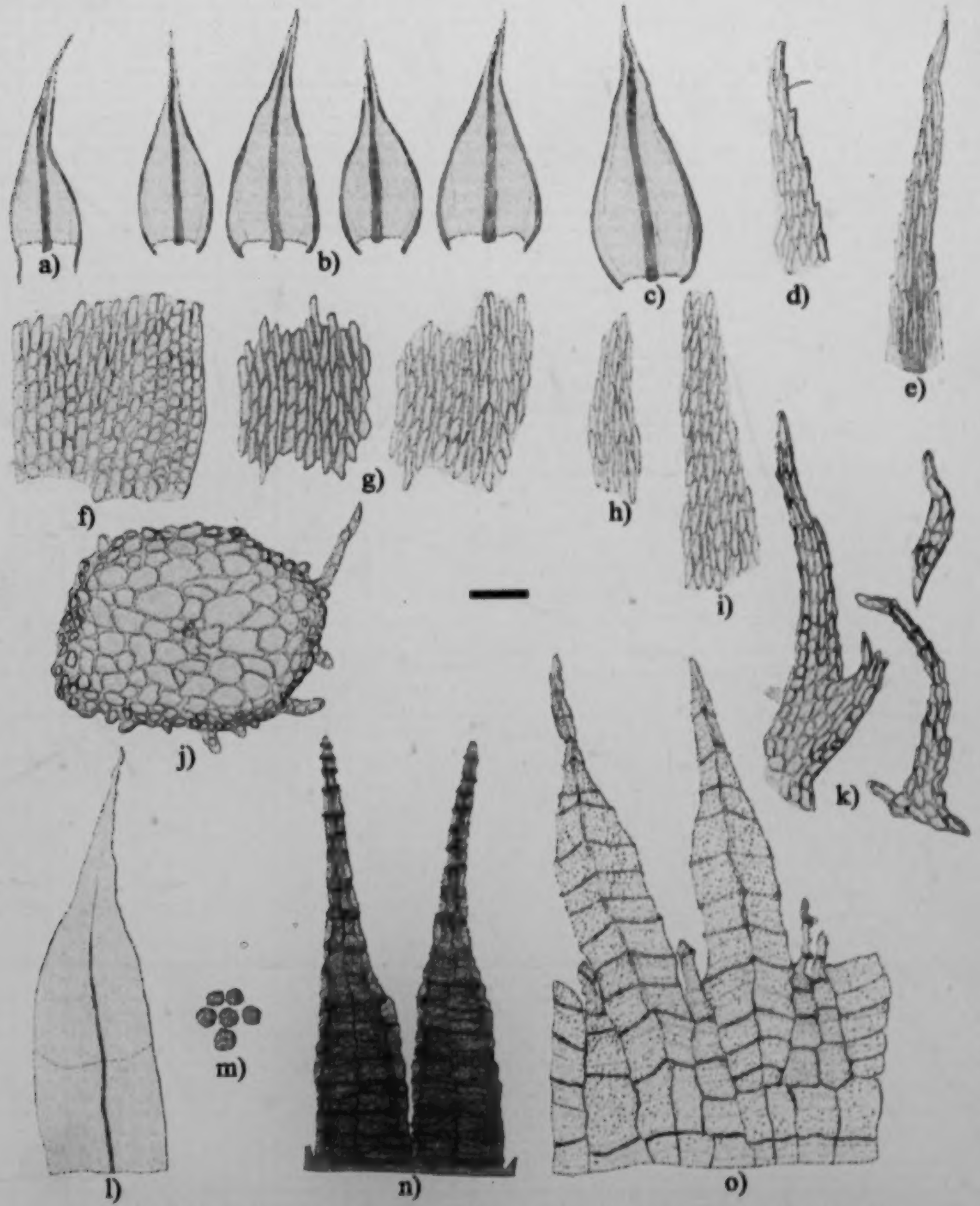
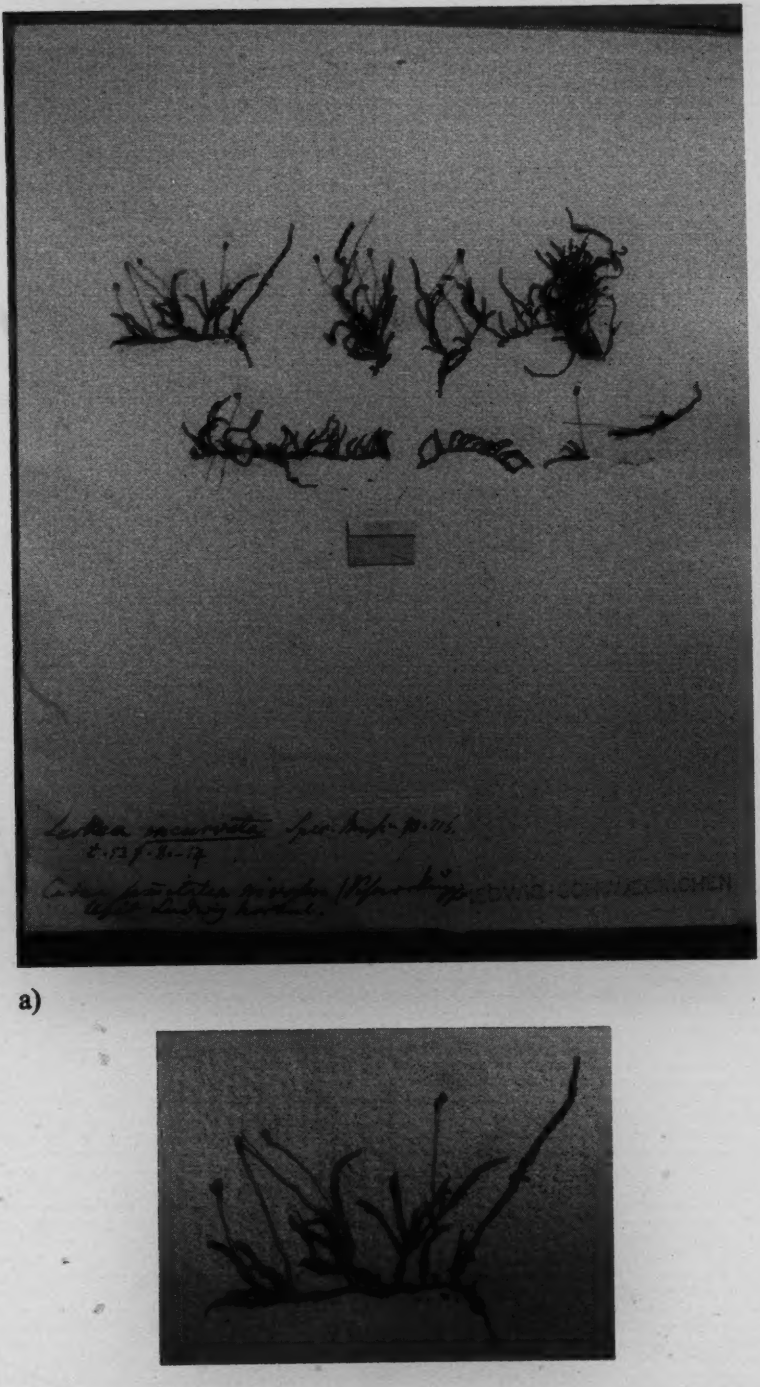


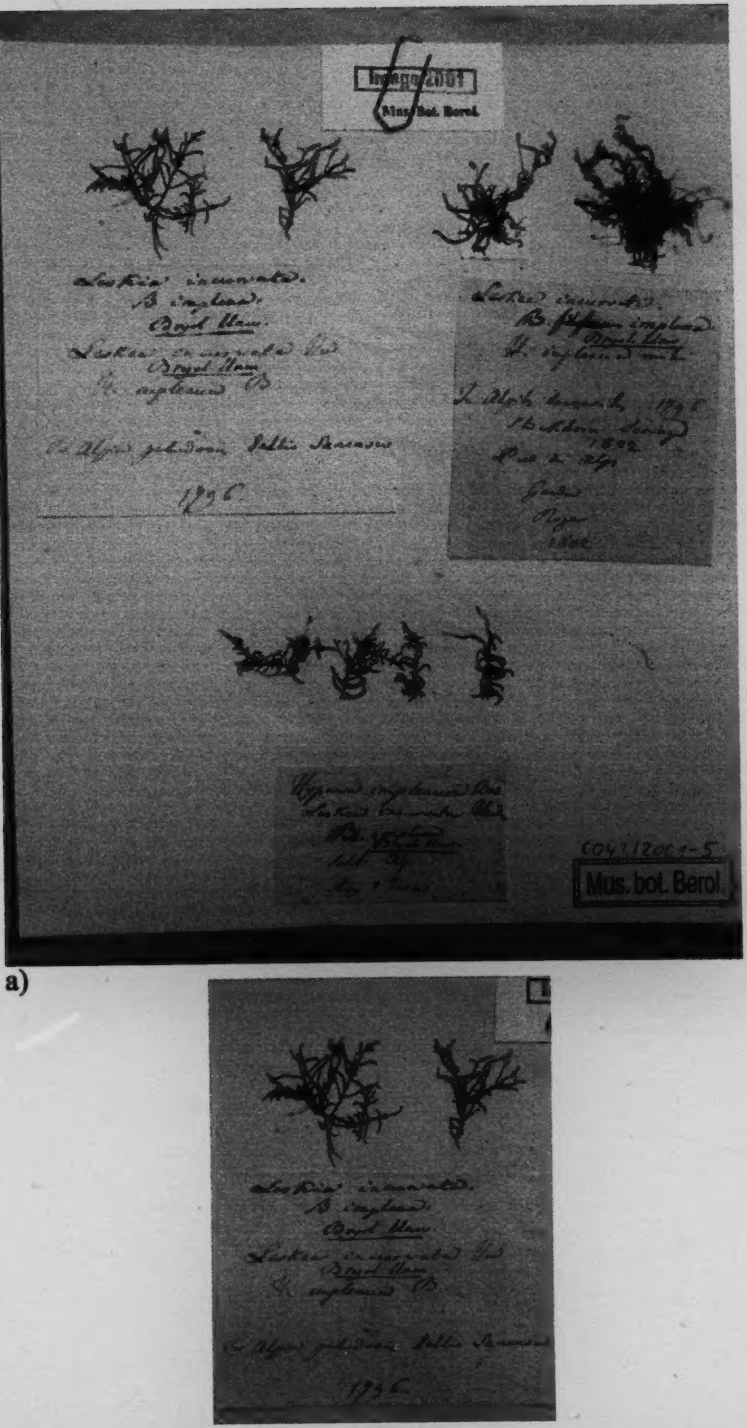
Figure 2.36. Illustrations of *Lescuraea radicosa* var *radicosa*: a)-c) stem leaves (*Hermann 24802* WTU, *Ireland 6010* WTU, *Flowers 2500* WTU); d),e) stem leaf apices (*Flowers 2500* WTU, *Hermann 24802* WTU); f),g) alar and basal, and median cells (*Hermann 24802* WTU); h),i) distal cells (*Hermann 24802* WTU, *Irleand 6010* WTU); j) stem transverse section (*Williams* F); k) paraphyllia (*Flowers 2500* WTU); l),m),n),o) inner perichaetial leaf, spores, exostome, and endostome (*Hermann 20581* WTU). Scale bar = 316 μm for a)-c),l); 48 μm for d)-k),m)-o).


Leskea incurvata Spec. Musc. p. 216.
t. 52 f. 8.-17

a)

b)

Figure 2.23. Digital images of *Leskea incurvata*: a) herbarium sheet with lectotype and syntypes; b) lectotype. Images from *Hedwig* G.


Mus. bot. Berol.
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a)

b)

Figure 2.24. Digital images of *Hypnum implexum*: a) herbarium sheet with lectotype and syntypes; b) lectotype. Images from *Bridel* B.

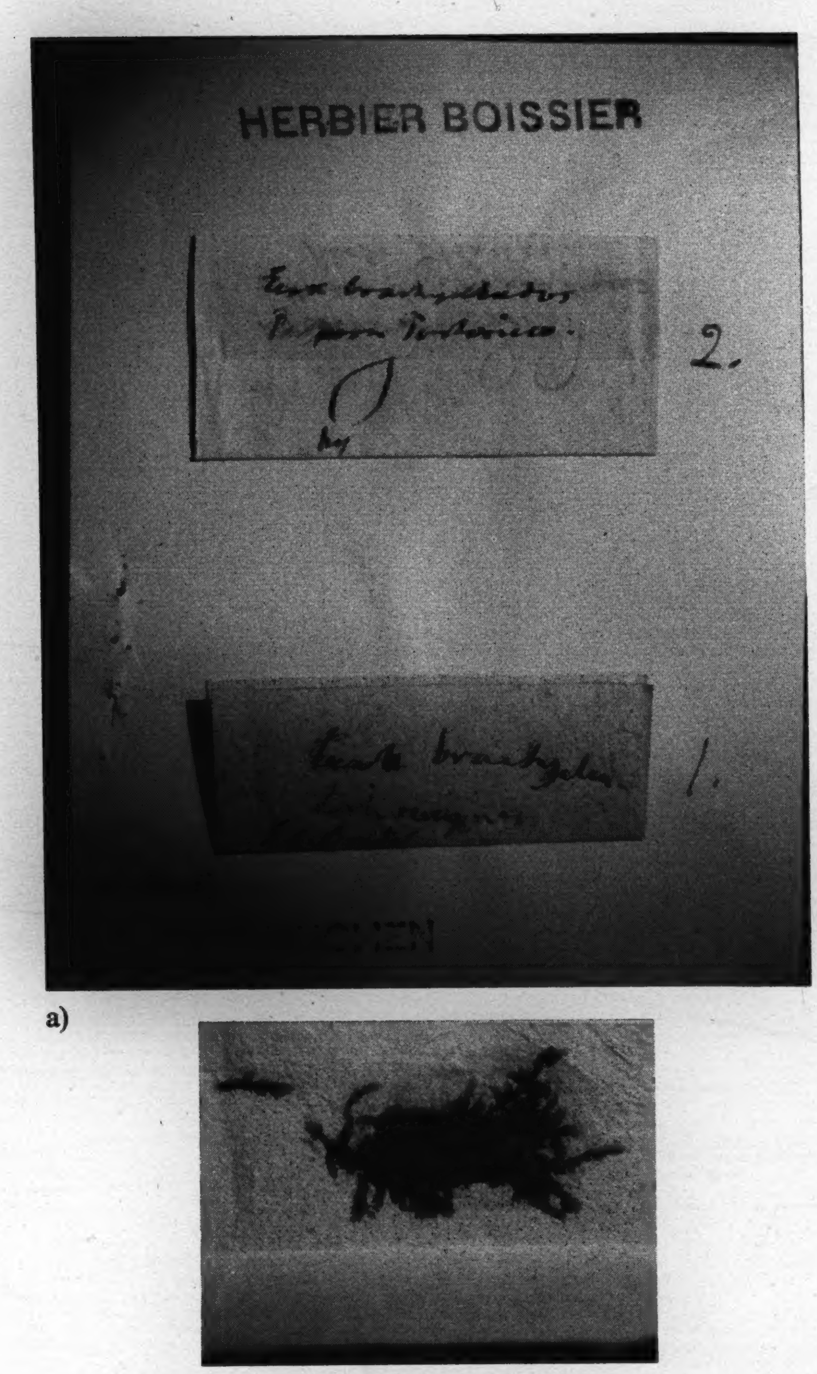
HERBIER BOISSIER
2.
1.
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Figure 2.37. Digital images of *Leskea brachyclados*: a) herbarium sheet with lectotype (as 1.) and another species (as 2.); b) lectotype. Images from *Schwägr.* in *Schultes* G.

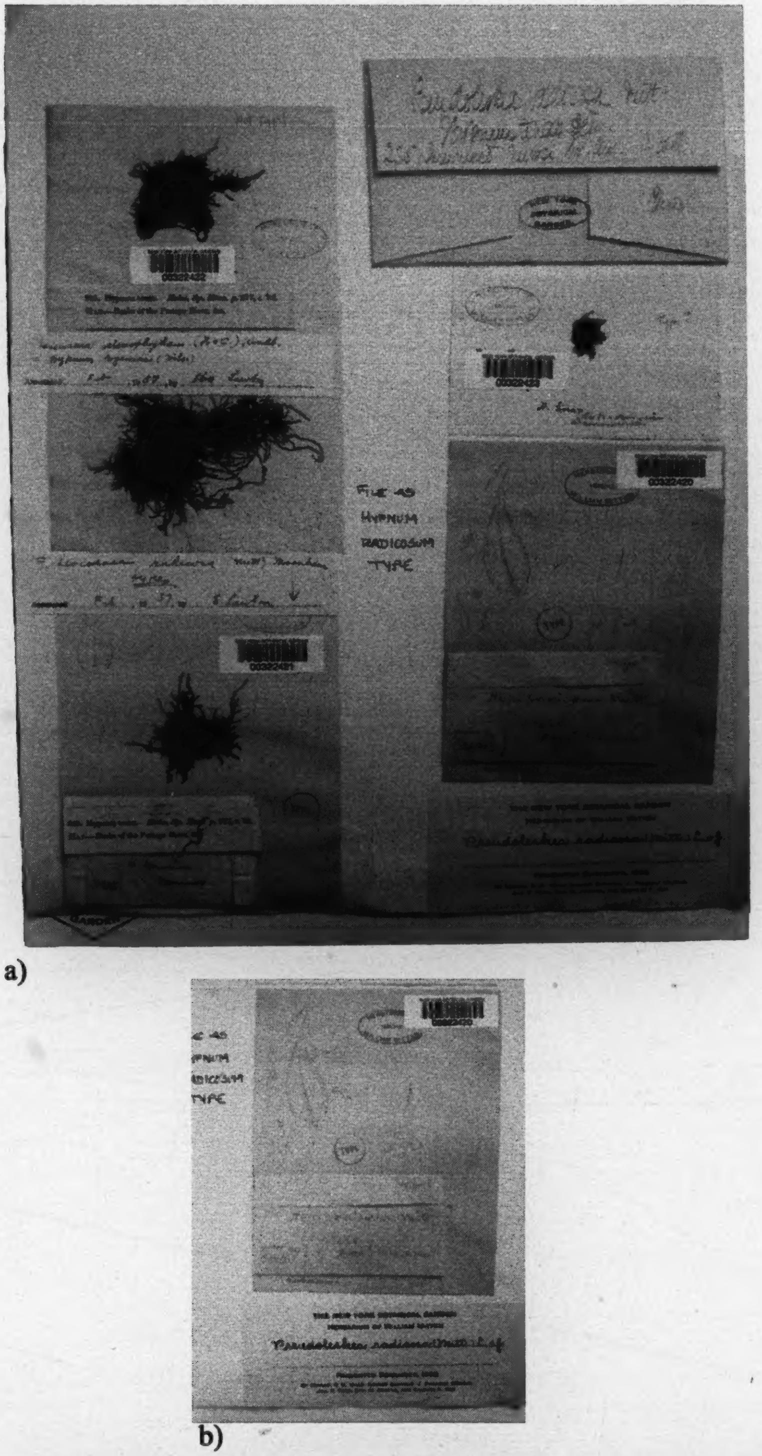
FILE AS
HYPNUM
RADICOSUM
TYPE
a)
b)

Figure 2.38. Digital images of *Hypnum radicosum*: a) herbarium sheet with lectotype and syntypes; b) lectotype. Images from *Drummond* NY.

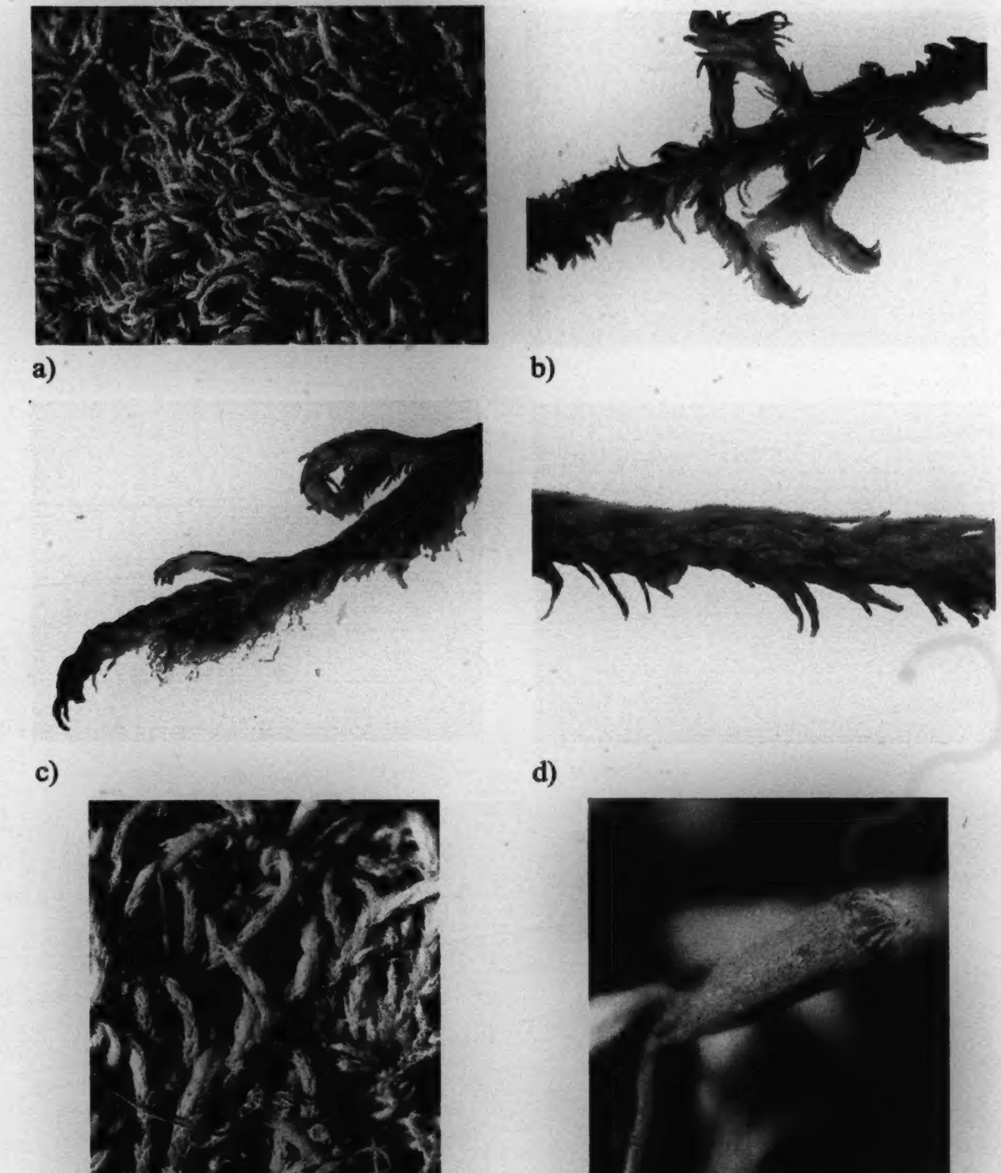

Figure 2.39. Digital images of *Lescuraea radicosa* var. *radicosa*: a) habit; b) stem with branches; c) stem apex; d) portion of stem; e) sporophytes; f) capsule with endostome revealed. All images from *Krieger & Hebben 1795* ALTA. Images taken at 60X (a), 250X (b,c,e), 500X Mag. (d,f).

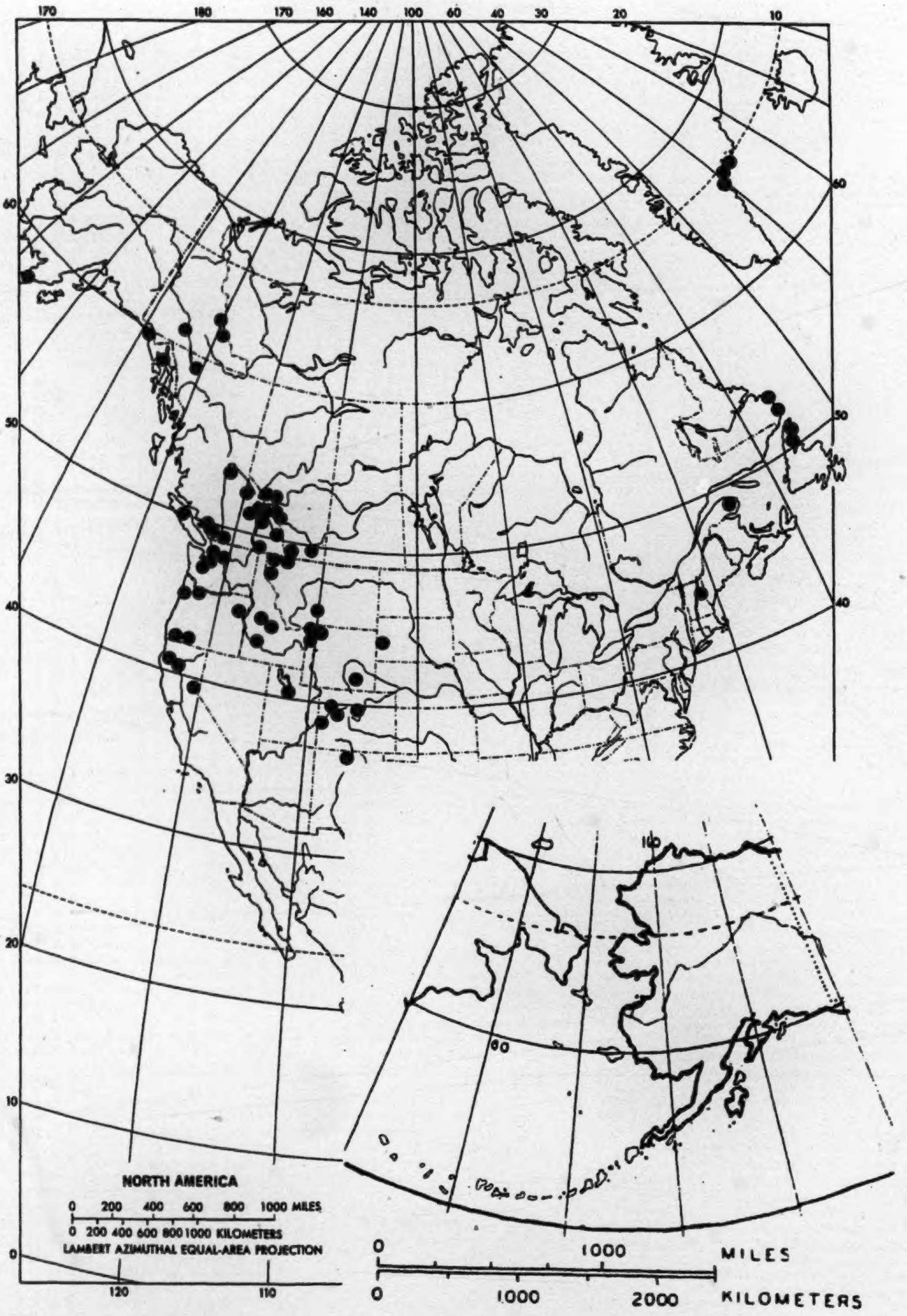
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Figure 2.40. Distribution of *Lescuraea radicosa* var. *radicosa*

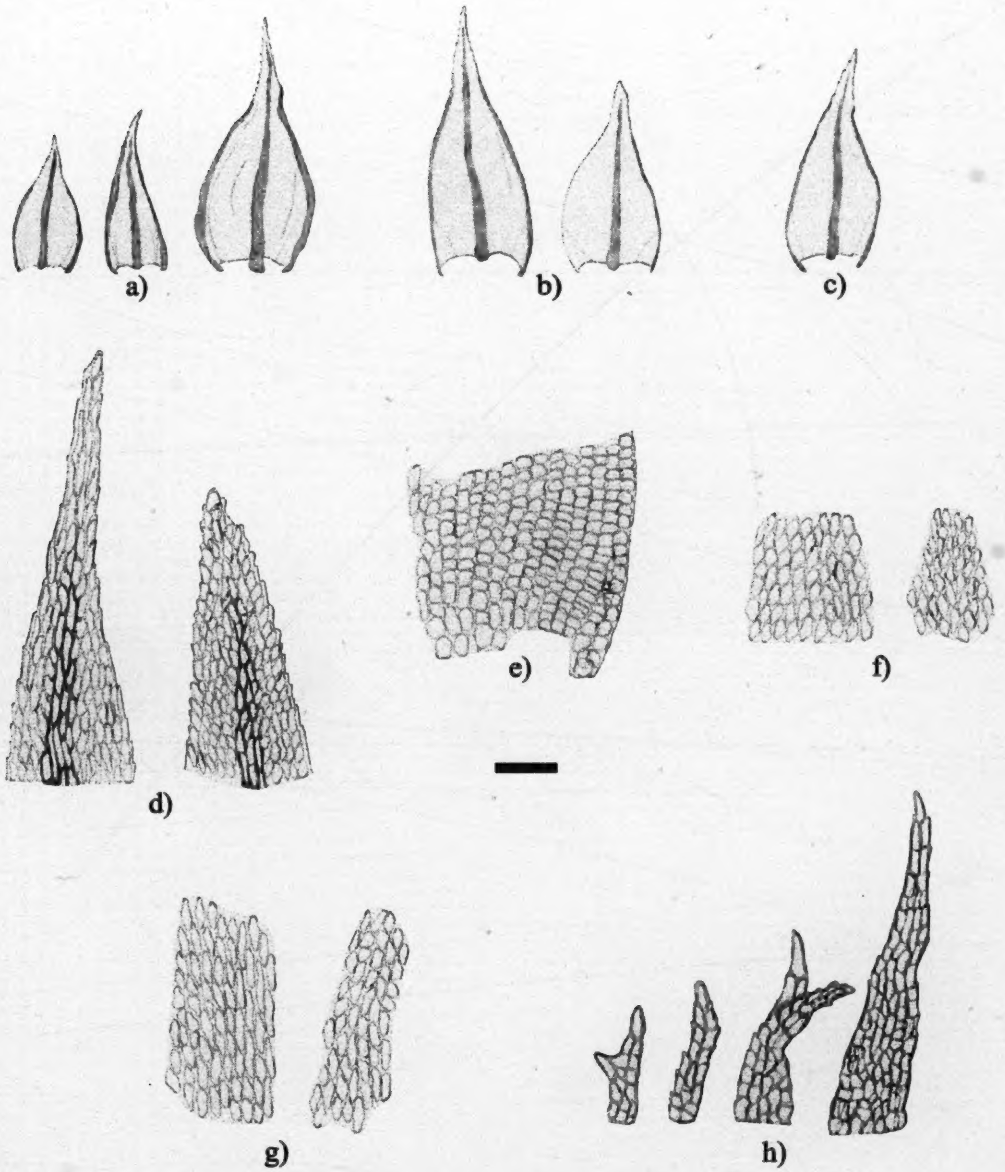

Figure 2.41. Illustrations of *Lescuraea radicosa* var. *compacta*: a)-c) stem leaves (*Macoun 340* HOLOTYPE NY, *Jones 10990* WTU, *Douglas 6998* WTU); d) stem leaf apices (*Jones 10990* WTU); e) alar and basal cells (*Macoun 340* HOLOTYPE NY); f),g) median and and distal cells (*Macoun 340* HOLOTYPE NY); h) paraphyllia (*Jones 10990* WTU). Scale bar = 316 μm for a)-c); 48 μm for d)-h).

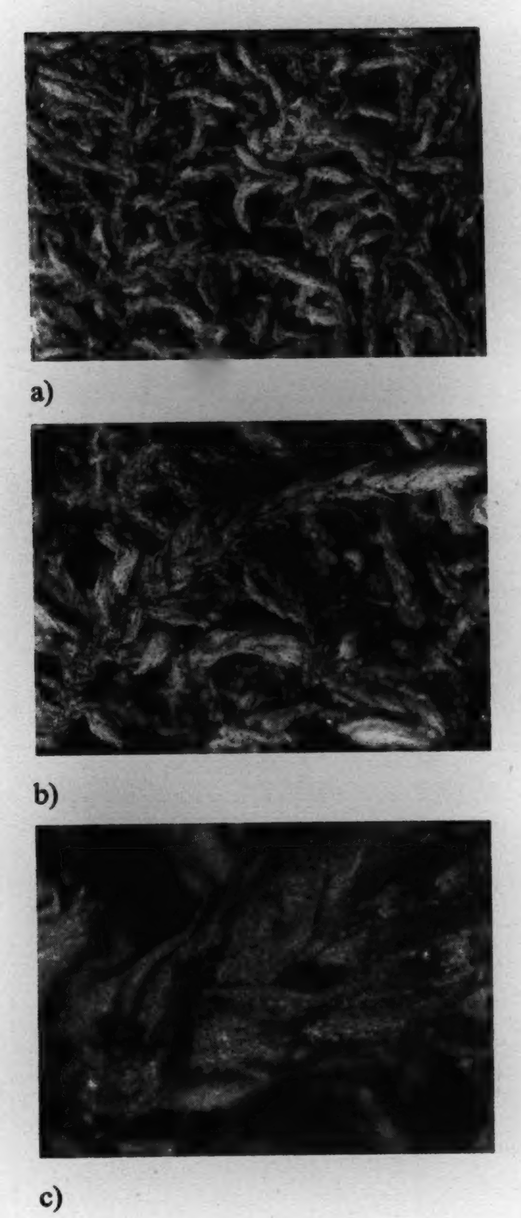

Figure 2.42. Digital images of *Lescuraea radicosa* var. *compacta*: a) habit; b) stem;c) portion of stem. All images from *Macoun* HOLOTYPE S. Images taken at 60X (a), 120X (b), 500X Mag. (c).

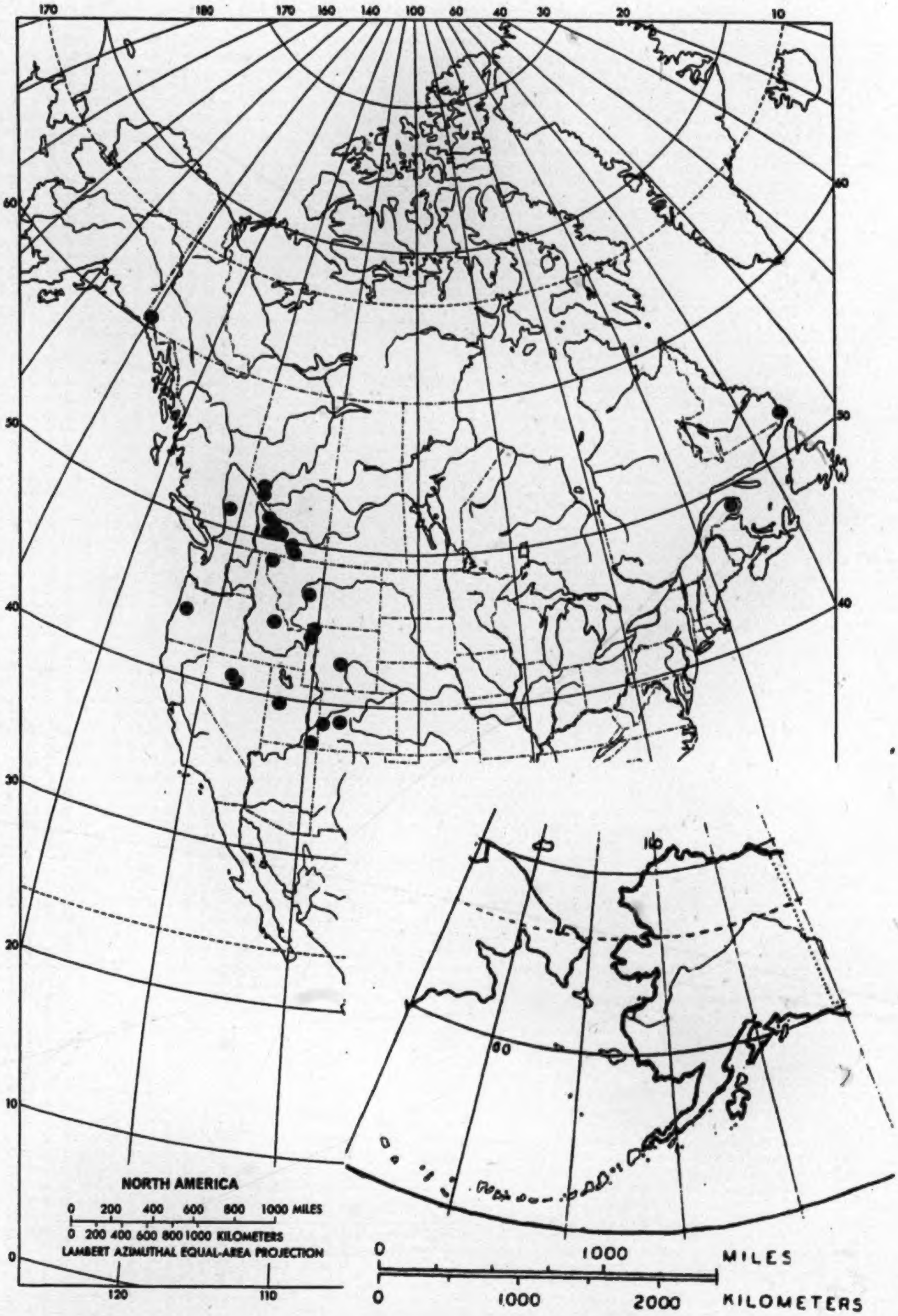
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Figure 2.43. Distribution of *Lescuraea radicosa* var. *compacta*

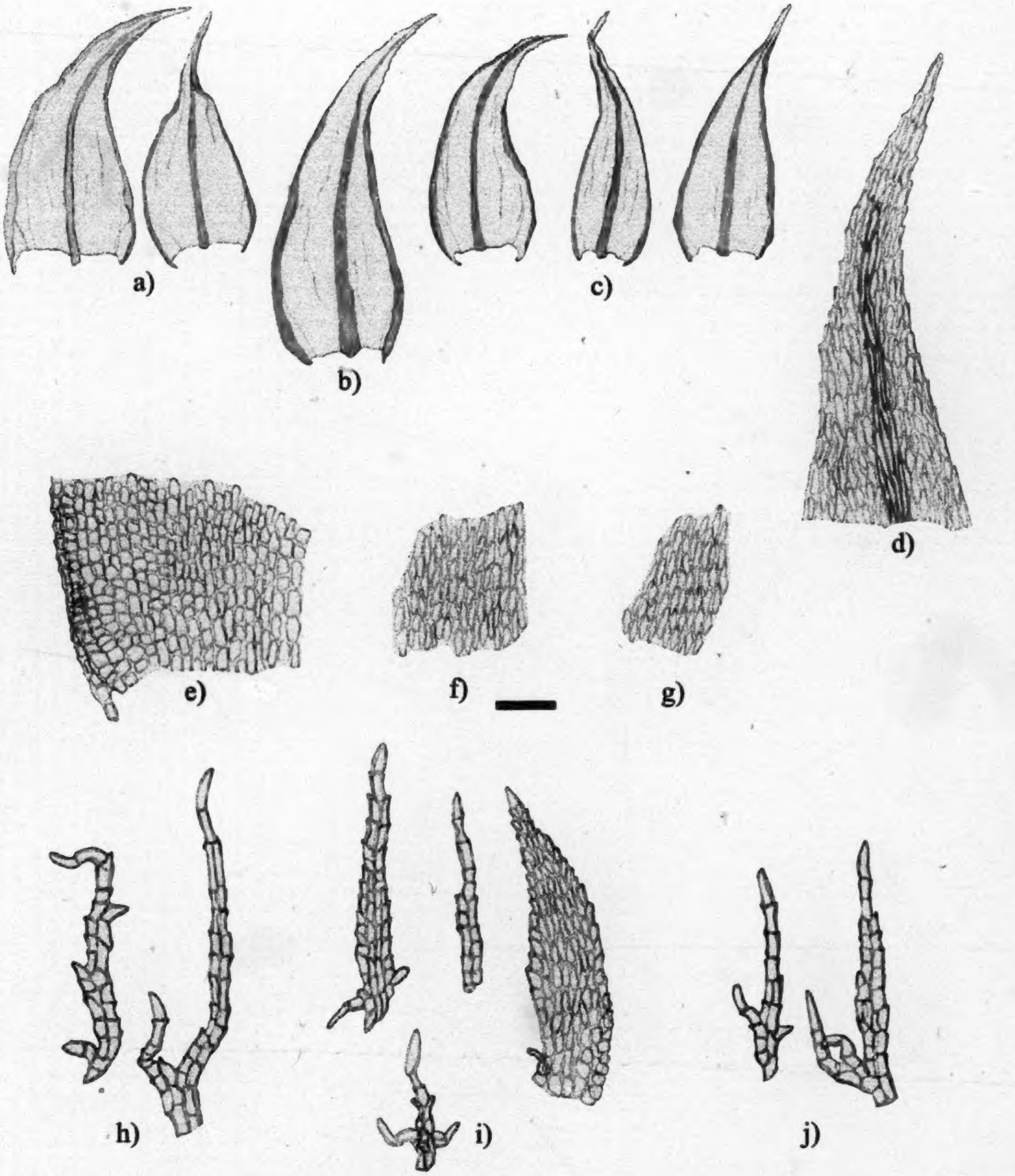

Figure 2.44. Illustrations of *Lescuraea radicosa* var. *denudata*: a)-c) stem leaves (*Macoun* LECTOTYPE S); d) stem leaf apex (*Macoun* LECTOTYPE S); e),f),g) alar and basal, median, and distal cells (*MacFadden 17981* MO); h)-j) paraphyllia (*Schofield & Godfrey 97881* UBC, *MacFadden 17981* MO, *Krieger 1750* ALTA). Scale bar = 316 μm for a)-c); 48 μm for d)-j).

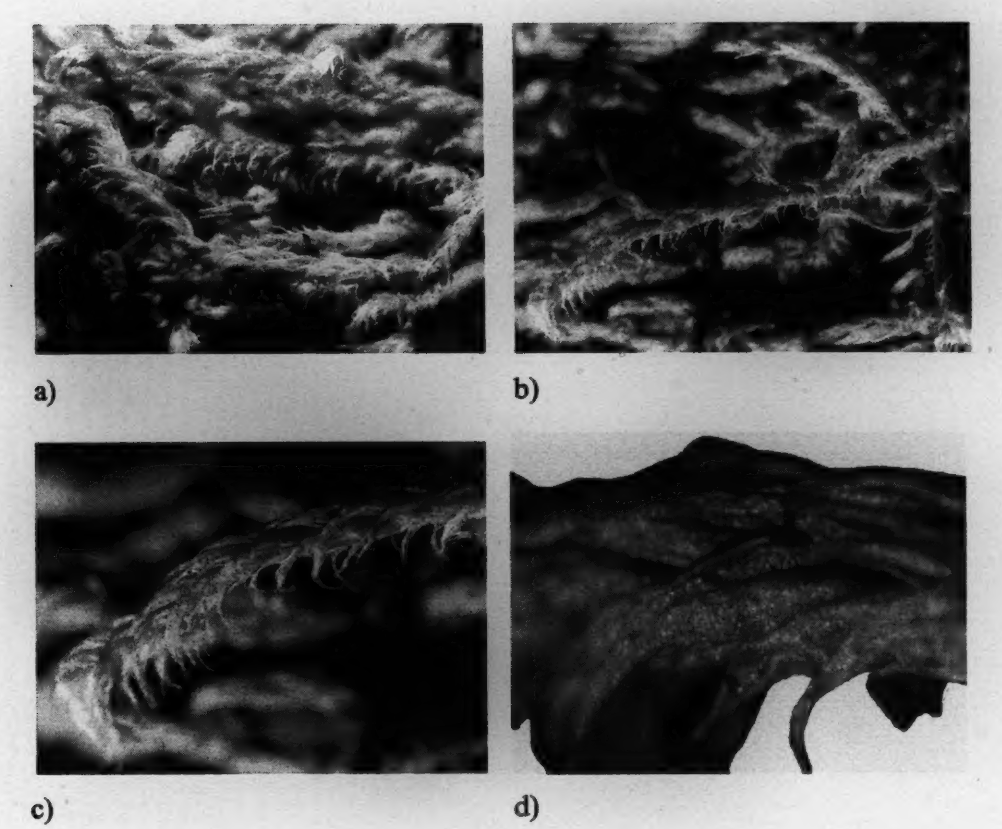

Figure 2.45. Digital images of *Lescuraea radicosa* var. *denudata*: a) habit; b) stem; c) stem showing apex; d) portion of stem. All images from *Krieger 1563* ALTA. Images taken at 60X (a,b), 120X (c), 500X Mag. (d).

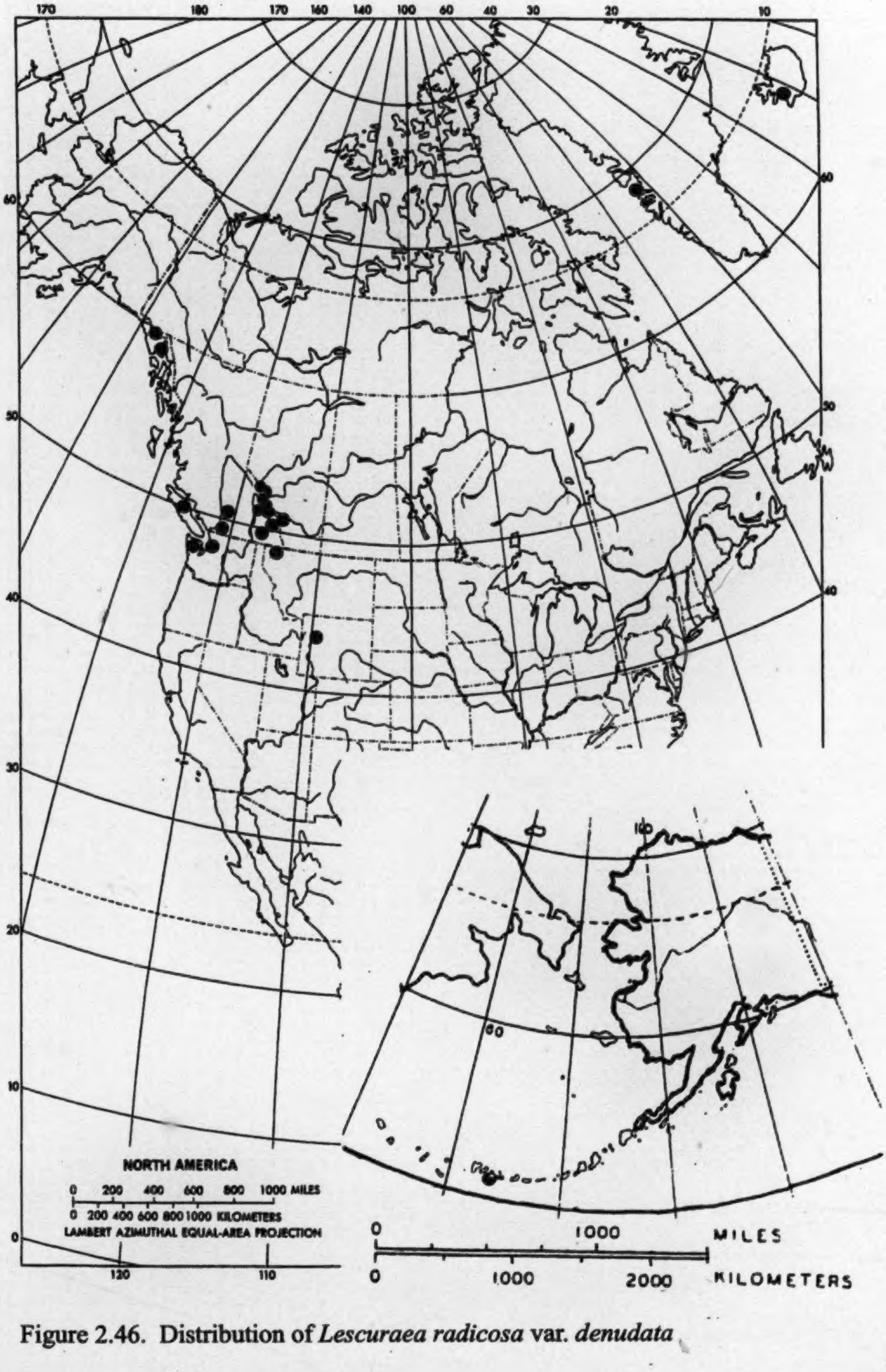
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Figure 2.46. Distribution of *Lescuraea radicosa* var. *denudata*

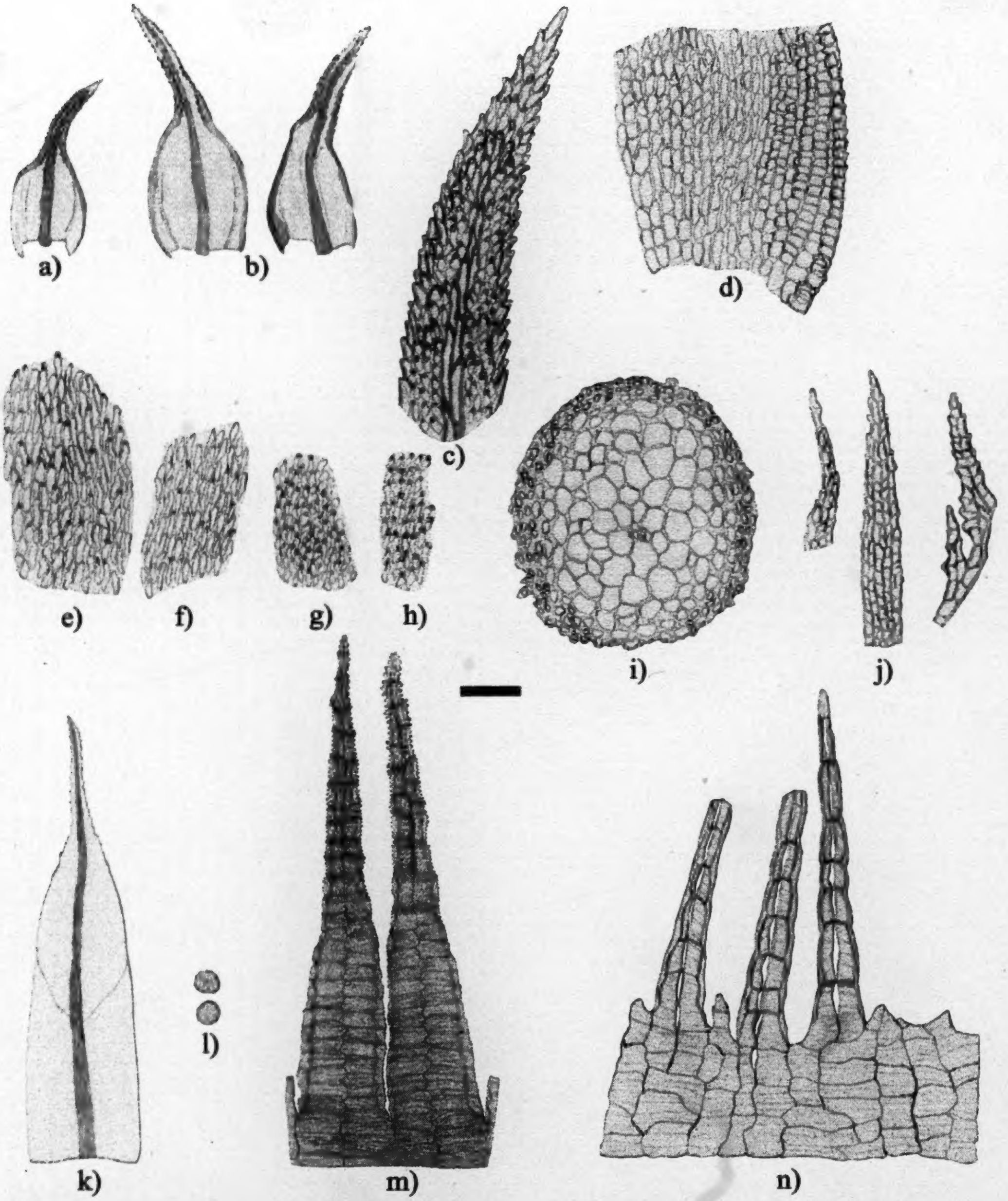

Figure 2.47. Illustrations of *Lescuraea saviana*: a),b) stem leaves (*Boros 4691* COLO, *Baumgartner 1226* CANM); c) stem leaf apex (*Boros 4691* COLO); d) alar and basal cells (*Boros 4691* COLO); e),f) median cells (*Boros 4691* COLO, *Baumgartner 1226* CANM); g),h) distal cells (*Boros 4691* COLO, *Baumgartner 1226* CANM); i) stem transverse section (*Glowacki* WTU); j) paraphyllia (*Boros 4691* COLO); k),l),m),n) inner perichaetial leaf, spores, exostome, and endostome, respectively (*Baumgartner 1226* CANM). Scale bar = 316 μm for a),b),k); 48 μm for c)-j),l)-n).

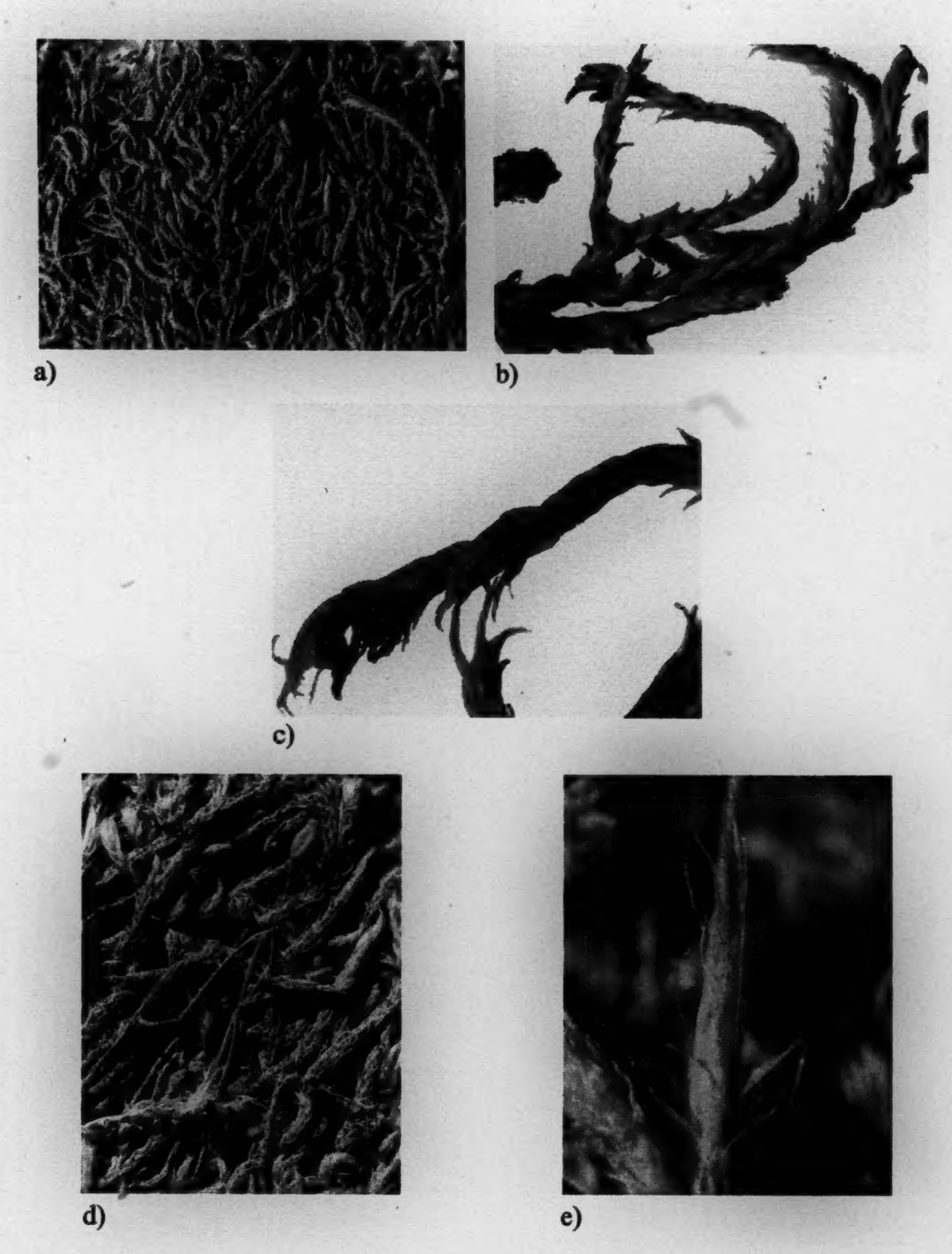

Figure 2.48. Digital images of *Lescuraea saviana*: a) habit; b) stems; c) portion of stem showing apex and rhizoids; d) sporophyte; e) perichaetium. All images from *Boros 4691* COLO. Images taken at 60X (a), 120X (d), 250X (b), 500X Mag. (c,e).

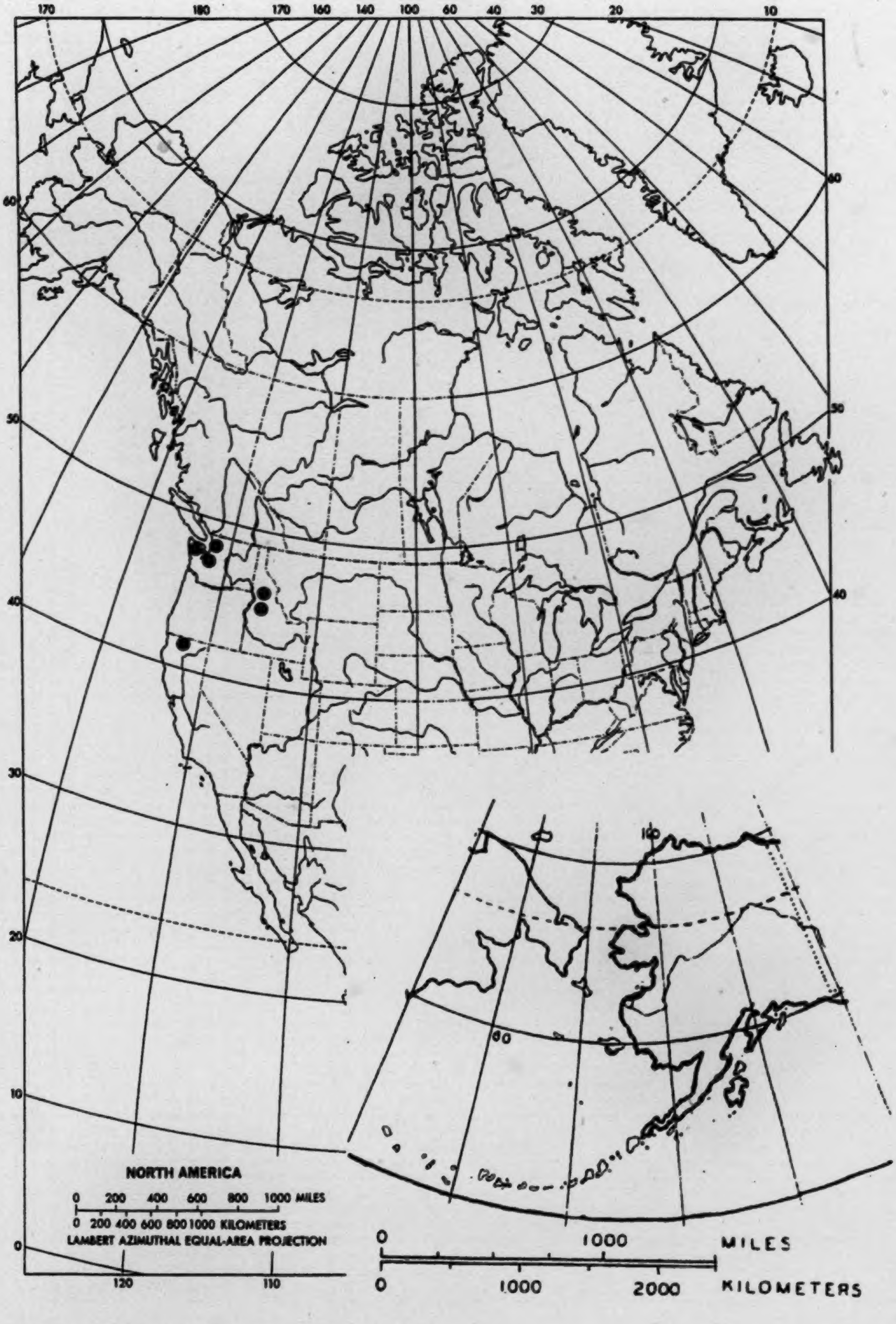
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Figure 2.49. Distribution of *Lescuraea saviana*

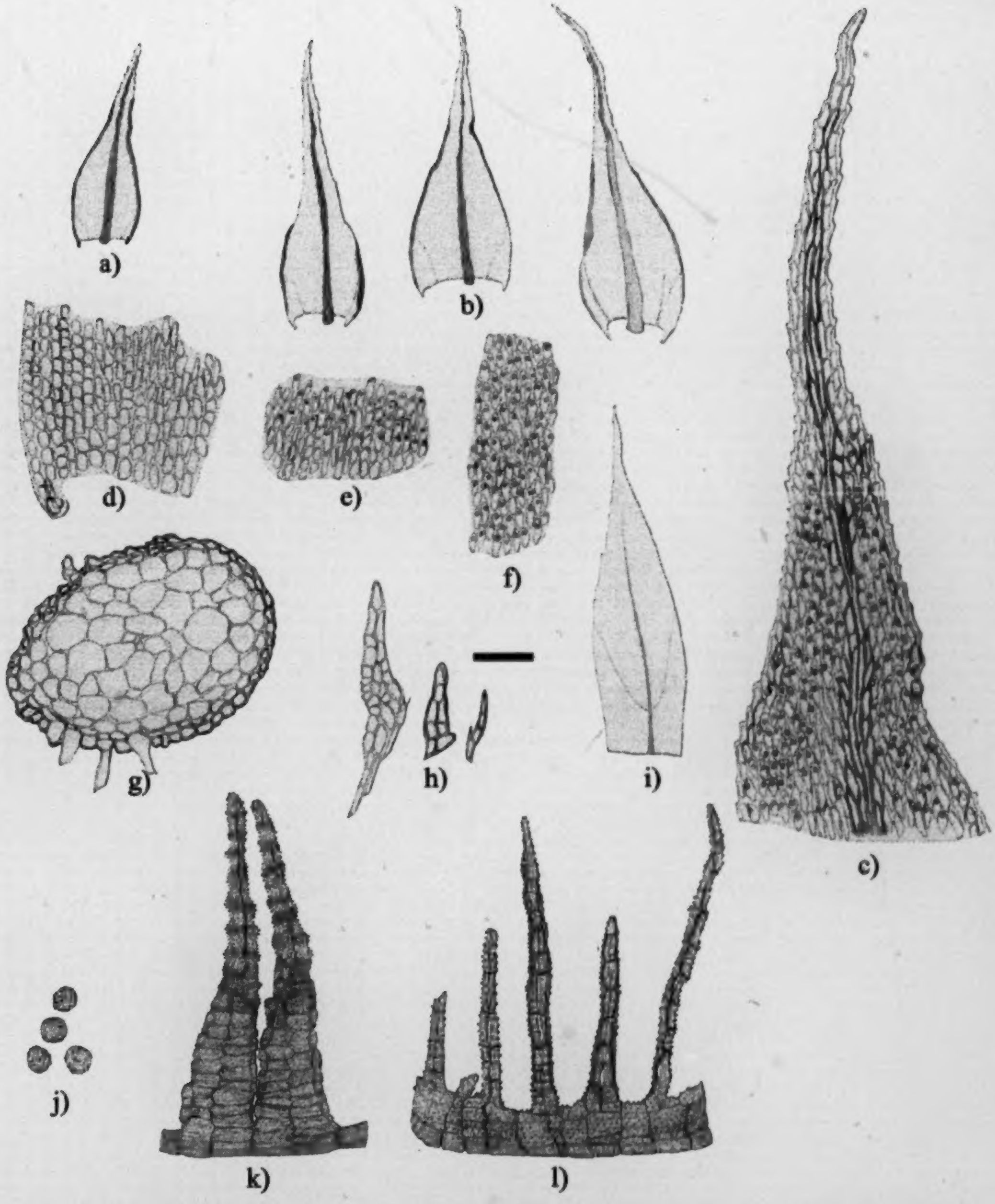
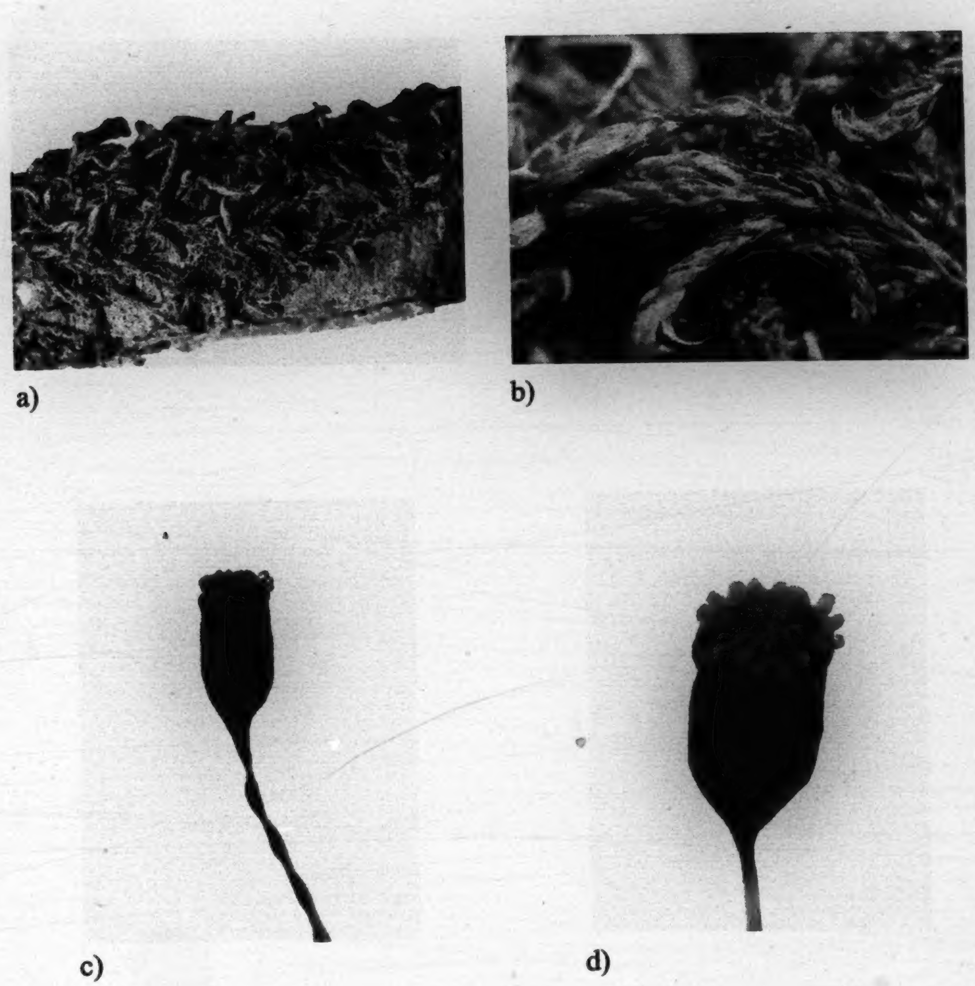


Figure 2.50. Illustrations of *Lescuraea stenophylla*: a),b) stem leaves (*Harpel 12796* WTU, *Hasselbach* ALA); c) stem leaf apex (*Hasselbach* ALA); d),e),f) alar and basal, median, and distal cells (*Harpel 12796* WTU); g) stem transverse section (*Schofield, Belland & Clayden 88386* UBC); h) paraphyllia (*Schofield, Belland & Clayden 88386* UBC); i) inner perichaetial leaf (*Schofield, Belland & Clayden 88386* UBC); j),k),l) spores, exostome, and endostome, respectively (*Allen 434* WTU). Scale bar = 316 µm for a),b),i); 48 µm for c)-h),j)-l).



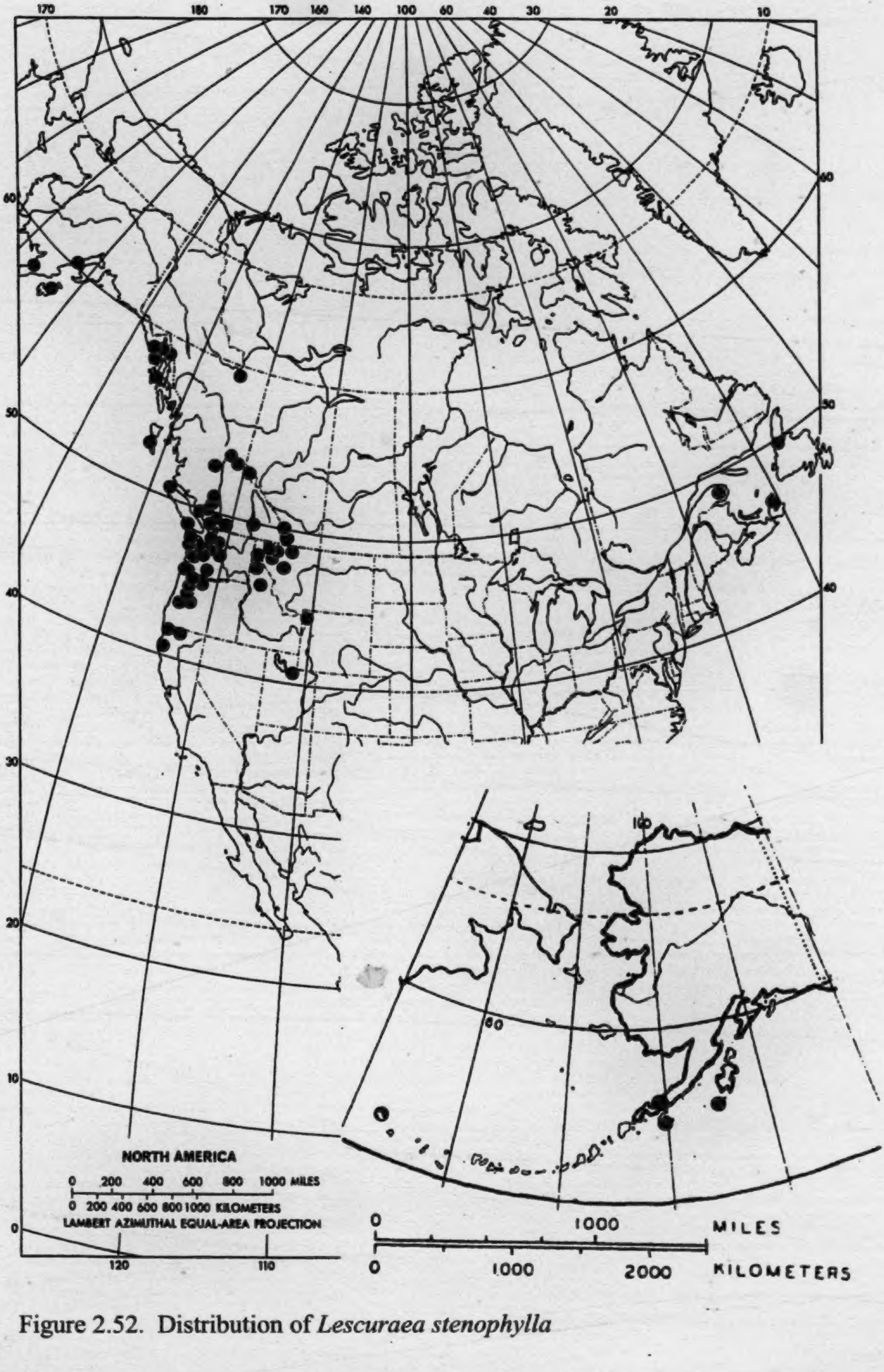
a)

b)

c)

d)

Figure 2.51. Digital images of *Lescuraea stenophylla*: a) habit; b) stems; c) sporophyte; d) capsule revealing peristome. All Images from *Krieger & Hebben 1801* ALTA. Images taken at 60X(a), 250X (b,c), 500X Mag. (d).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0 1000 2000 KILOMETERS

Figure 2.52. Distribution of *Lescuraea stenophylla*

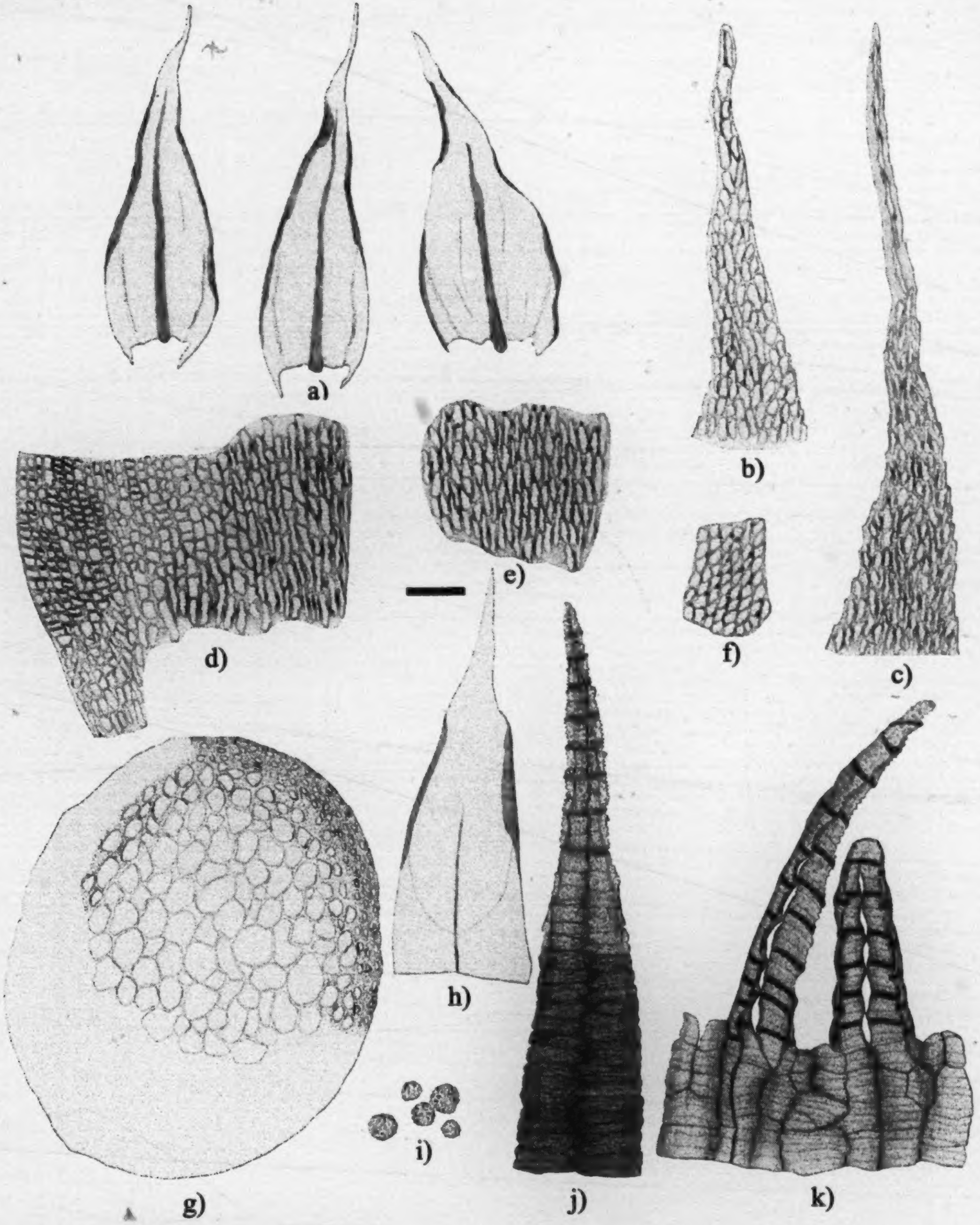
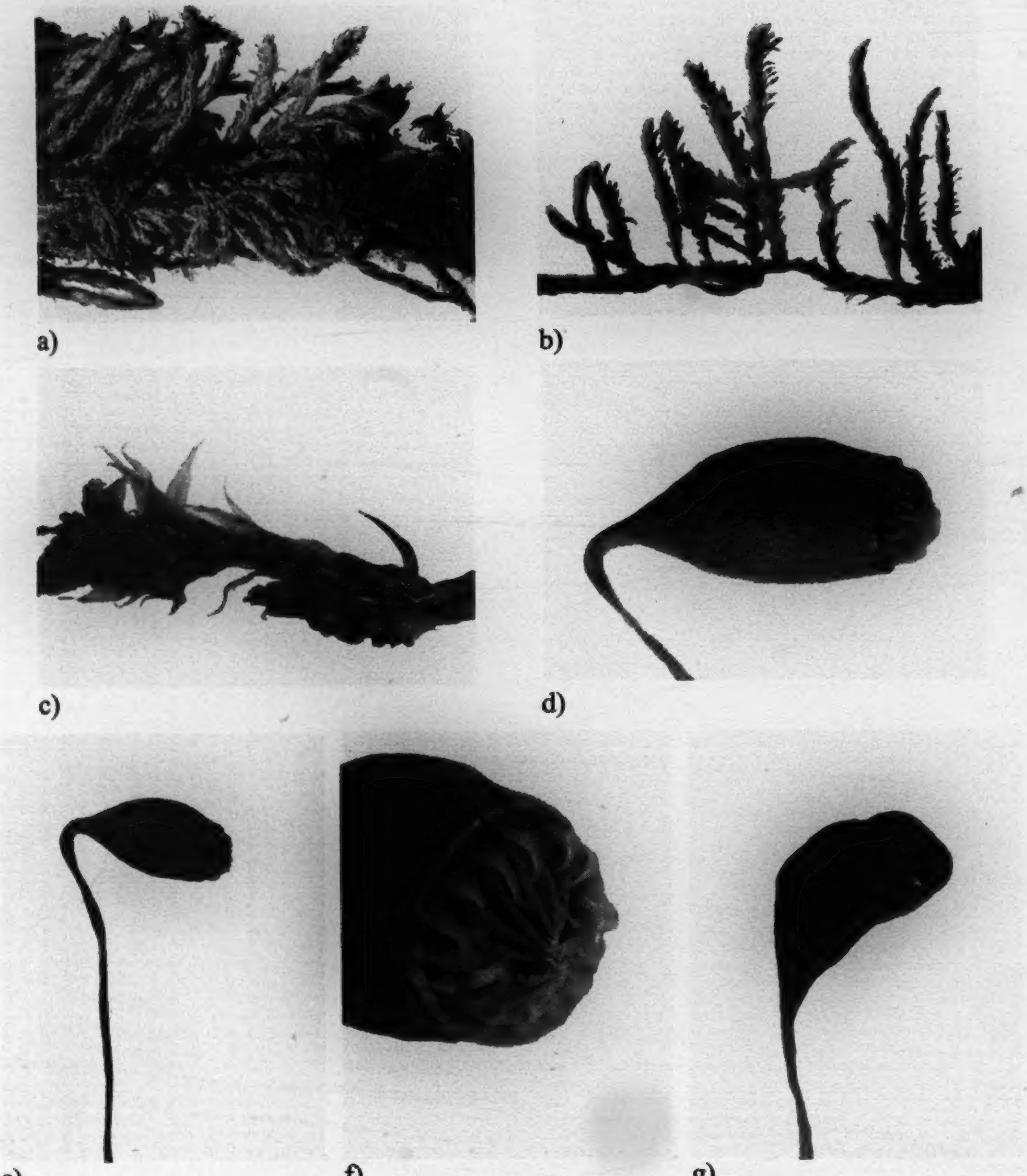
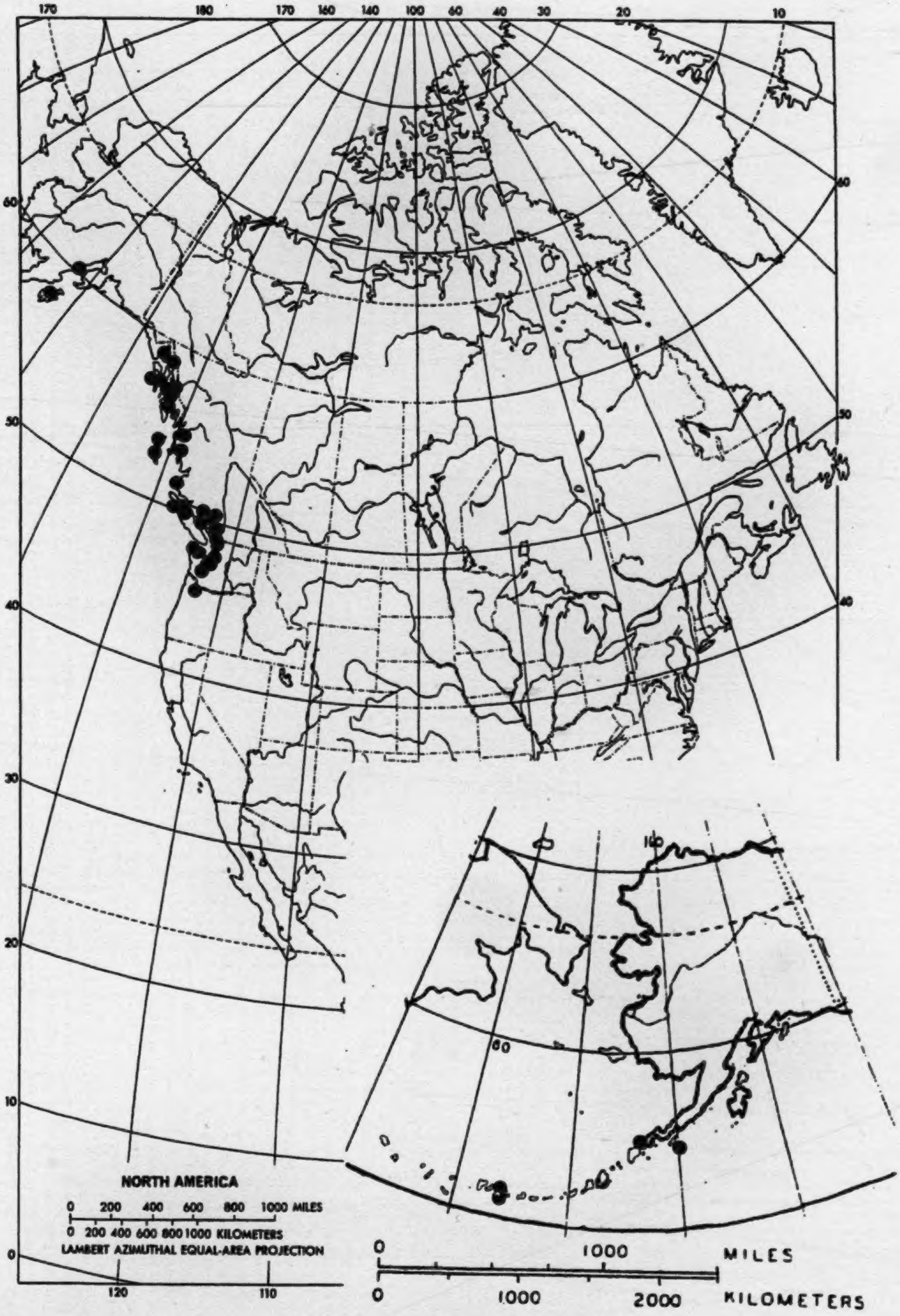


Figure 2.53. Illustrations of *Rigodiadelphus baileyi*: a) stem leaves (*Bailey* NY); b),c) stem leaf apices (*Schofield 71448* F, *Hermann 18458* US); d),e),f) alar and basal, median, and distal cells (*Schofield 71448* F); g) stem transverse section (*Schofield 71448* F); h) inner perichaetial leaf (*Schofield 71448* F); i),j),k) spores, exostome, and endostome, respectively (*Worley & Boas 11503* MO). Scale bar = 316 µm for a),h); 48 µm for b)-g), i)-k).



a) b) c) d) e) f) g)

Figure 2.54. Digital images of *Rigodiadelphus baileyi*: a) habit; b) stem and branches; c) stem apex; d) capsule; e) sporophyte; f) capsule revealing peristome; g) sporophyte with operculum. Images a)-c) from *Krieger & Hebben 1835* ALTA; d)-f) from *Schofield & Sharp 25792* CANM; g) from *Worley & Boas 11503* MO. Images taken at 60X (a), 120X (b,e), 250X (d,g), 500X Mag. (c,f).


170
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LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
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110
160
60
0
1000
MILES
0
1000
2000
KILOMETERS

Figure 2.55. Distribution of *Rigodiadelphus baileyi*

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Chapter 3

THE INFRAGENERIC CLASSIFICATION AND PHYTOGEOGRAPHY OF *LESCURAEA* BRUCH & SCHIMP. *IN* B.S.G.

3.1 The infrageneric classification of *Lescuraea* Bruch & Schimp. *in* B.S.G.

Based on various taxonomic concepts among researchers, the circumscription of infrageneric taxa in *Lescuraea* has differed. In order to illustrate this, three prominent classifications are depicted (Table 3.1). However, these are by no means exhaustive. Best (1900) was the first person to consider *Lescuraea* and *Pseudoleskea* to be congeneric, recognising *Lescuraea* as a subgenus of *Pseudoleskea*. Best (1900) accepted Kindberg's (1897) subgenus *Eu-Pseudoleskea*, and created subgenus *Radicosella* to accommodate the remaining taxa in *Pseudoleskea*. On the other hand, Brotherus (1907) recognised *Lescuraea* at the generic level. Under *Pseudoleskea*, Brotherus (1907) combined the two subgenera *Eu-Pseudoleskea* and *Radicosella*, and reduced *Eu-Pseudoleskea* to the rank of section. Then in 1957, Lawton reduced *Pseudoleskea* to a subgenus of *Lescuraea*, to accommodate many of the taxa within both *Eu-Pseudoleskea* and *Radicosella*. For a detailed discussion of the historical development of the genus, refer to Chapter 2.1. Based on the current taxonomic revision and partly on earlier classifications developed by Best, Brotherus, and Lawton, an infrageneric classification of *Lescuraea* is presented (Table 3.2). The current classification differs primarily from that of Lawton (1957), in that the monotypic subgenus *Tricholeskea* is not accepted at this rank, but has been transferred to the genus *Rigodiadelphus*.

In the proposed classification, I consider *Lescuraea* and *Pseudoleskea* to be congeneric, and recognise two subgenera within *Lescuraea*. What follows is a synopsis of the characters I used to define *Lescuraea* (including infrageneric taxa). I included an unrooted tree displaying my hypothesis of the relationships between some members of the Leskeaceae (Fig. 3.1). However, this tree should not be considered correct in a phylogenetic sense, since a cladistic analysis was not performed. It serves merely as a visual aid.

3.1.1. *Lescuraea* and *Rigodiadelphus*

The genus *Lescuraea* and the closely related taxon *Rigodiadelphus*, are linked by seven characters: 1) distinctly biplicate leaves; 2) recurved leaf margins; 3) leaf margins distally serrate to crenate; 4) quadrate to enlarged-quadrate alar cells; 5) papillose or prorate laminal cells; 6) distal, abaxially prorate costae; and 7) lack of an annulus connecting the operculum to the capsule mouth. This combination of characters is unique to these two genera, and reliably separates them from the genus *Pseudoleskeella sensu lato*, wherein some taxa in *Lescuraea* have occasionally been placed. Taxa in *Pseudoleskeella* all have plane and entire leaves, with transversely elongate or elliptic alar cells, smooth laminal cells and a smooth costa, and a distinct annulus connecting the operculum to the capsule mouth. Although the genus *Ptychodium* shares some characters (1, 2, 4, 7) with both *Lescuraea* and *Rigodiadelphus*, the relationship of this taxon to the latter two genera is unclear.

Rigodiadelphus

Rigodiadelphus is defined by eight characters: 1) leaves with a stout costa below, narrowing and ending abruptly in the upper leaf region; 2) stem transverse sections consisting of numerous (5-8) rows of very thick-walled, outer cortical cells, and 3) lacking a central strand; 4) paraphyllia lacking; 5) globose-cylindric capsules; 6) perichaetial leaves of the second type; 7) stem and branch leaves with hyaline hair points; and 8) distinctly pitted laminal cells.

Lescuraea

The genus *Lescuraea* is further defined by six characters: 1) leaves with a stout, keeled, and subpercurrent to percurrent costa; 2) stem transverse sections consisting of several (1-3) rows of outer cortical cells, including 3) a distinct central strand; 4) the presence of paraphyllia; 5) short-cylindric capsules; and 6) a hypnobryalean peristome (at various stages of reduction). Peristomial differences observed are attributed to reduction. Consequently, a range in the reduction of peristome parts can be seen. Although there are genera that exhibit some of these character states, no other genus exhibits this combination, including the characters shared by both *Lescuraea* and *Rigodiadelphus*.

The subgeneric delimitation of *Lescuraea* and *Pseudoleskea* is based primarily on peristomial characters.

Subgenus *Lescuraea*:

Subgenus *Lescuraea* accommodates two species (of those I examined) and is defined by the following characters: 1) a reduced hypnobryalean peristome inserted below the mouth of the capsule; 2) exostome teeth with horizontal ridges in the proximal region, and 3) coarse, densely distributed papillae in the distal region; 4) filiform and coarsely papillose endostomial segments; 5) perichaetial leaves of the second type; and 6) erect, symmetric capsules. The character states associated with the peristome in subgenus *Lescuraea* are shared by both taxa, which may prove to be a synapomorphy in a later cladistic analysis. Consequently, I believe that *L. mutabilis* evolved from a common ancestor with *L. saxicola*, as plants became epiphytic. *Lescuraea mutabilis* features a more reduced peristome, including slight 2° ornamentation on the OPL surface of the exostome. In addition, the exostome is distinctly perforated by round holes along the median line. However, the perichaetial leaves in this taxon are clearly of the first type, being linear and possessing a stout, excurrent costa. Since all other taxa in *Lescuraea* possess perichaetial leaves of the first type, the perichaetial leaves in *L. saxicola* (second type), with recurved to squarrose leaves that include a very weak costa ending mid-leaf or below, may represent a lost character.

Subgenus *Pseudoleskea*:

Subgenus *Pseudoleskea* accommodates six species (of those I examined) and is delimited by five characters: 1) a hypnobryalean peristome inserted along the mouth of the capsule, and at varying stages of reduction; 2) exostome teeth with horizontal papillose-striae or fine striae in the proximal region, and 3) round, sparsely distributed papillae in the distal region; 4) type one perichaetial leaves; and 5) arcuate or suberect and asymmetric capsules (some erect and symmetric). Based on the extent of peristome reduction and perichaetial leaf variation, two smaller groups may be further classified within subgenus *Pseudoleskea*. Although I do not rank these two groups in the proposed classification, the first group accomodates *Lescuraea patens* and *L. atricha*, which have more hypnobryalean peristomes, including an endostome with a high basal membrane and long, filiform cilia. The perichaetial leaves in these two taxa are clearly of the first type, being linear-lanceolate and abruptly acuminate, and possessing a stout, percurrent costa. Gametophytically, they are dissimilar in many character states, and I cannot speculate over the relationship between these two taxa at this time. Taxa in the second group, accommodating *L. incurvata sensu lato*, *L. radicosa sensu lato*, *L. saviana*, and *L. stenophylla*, have semi-reduced or reduced peristomes, including an endostome with a medium or low basal membrane, short and blunt cilia or cilia lacking. The perichaetial leaves in these taxa are also of the first type, but the leaves are lanceolate and gradually acuminate, the costa is weaker and ends in the upper leaf or sometimes percurrent. The only exception to this is that the perichaetial leaves of *Lescuraea saviana* resemble those of *L. patens*, *L. atricha*, and *L. mutabilis*. Consequently, the relationship between taxa in this second group is unclear. Although I can speculate that *L. incurvata sensu lato* and *L. radicosa sensu lato* evolved from a common ancestor, I am uncertain about the evolution of *L. saviana*. *Lescuraea saviana* appears intermediate between the two aforementioned taxa in many character states, and it even features a more reduced peristome. Conversely, I believe *Lescuraea stenophylla* evolved from a common ancestor with *L. radicosa* var. *radicosa*. However, based on speculation over relationships between taxa in both groups, I decline in ranking them any further, and maintain them as a single group in subgenus *Pseudoleskea*.

The current taxonomic treatment of *Lescuraea* and *Pseudoleskea* is a revision of the North American taxa. A future revision of an additional 16 taxa (Table 3.3) would complete a monograph of the genus, and set the stage for a phylogenetic analysis of the morphological characters. This would provide an evolutionary perspective of the genus. A cladistic analysis of morphological characters would clarify the subgeneric taxa and provide additional data for the current classification. Further, a species phylogeny would potentially elucidate relationships within each subgenus, thus warranting a more detailed classification.

3.2. The distribution and diversity of *Lescuraea* Bruch & Schimp. *in* B.S.G.

The earliest fossil moss recognised by many researchers, including Miller (1982) is *Muscites plumatus* from Lower Carboniferous shales of the forest of Dean, Gloucestershire. While many pre-Permian (> 300 myr BP) plant remains have been discovered, it is questionable whether they are indeed bryophytic (Miller 1982). *Muscites plumatus* on the other hand, revealed sufficient cellular detail to show it comparable to true mosses. *Muscites polytrichaceus* and *M. bertrandii* are pre-Permian mosses from the Stéphanien strata (Upper Carboniferous) of France (Miller 1982). Reports of Triassic (240-210 myr BP) mosses are few. However, Anderson (1976) discovered *Muscites guescelinii* at several sites, including eight perfectly preserved *in situ* moss cushions.

The first fossil moss remains of the Cretaceous (135-64 myr BP) discovered was that of *Muscites lesquereuxii* from Tennessee (Miller 1982). Subsequently, Brown and Robison (1974) found a well-preserved moss, *Diettertia montanensis*, in the Lower Cretaceous of Montana. At this time, a number of species of *Sphagnum* were reported from northeast Russia and from southeast United States (Miller 1982).

Angiosperms dominated the vegetation at the beginning of the Tertiary (64-40 myr BP). However, the groups of bryophytes that had diversified in the Cretaceous, adapted to the abundance of mesic to humid niches associated with hardwood forests (Miller 1982). Consequently, with the radiation of angiosperms, corticolous bryophytes began to evolve. According to Vitt (1995) dispersal and diversification of extant corticolous taxa in *Calomnion* (Calomniaceae) throughout Australasia and the South Pacific, appears to have occurred within the past 30-20 million years. Buck (1991) proposed "that pleurocarpous mosses are of more recent origin than acrocarps," an assumption based on pure circumstance, but attributed to several facts. First, "there are no isolated, single-species families," owing to recent divergence; second, "pleurocarps generally grow in sheltered, forest habitats"; and third, "most ...acrocarpous families are cosmopolitan (Pangaean) ... whereas most ...pleurocarpous families are either Gondwanan or Laurasian in dispersal." Buck (1991) speculated that "angiospermous habitats were present before the evolution of mosses," and that "Pangaean taxa are of more ancient origin."

According to Dickson (1973), most of the mosses of the European Miocene appear identical to the genera and even species that now occur on that continent. For example, terricolous and saxicolous fossil Miocene (25-13 myr BP) pleurocarpous bryophytes reported by Jovet-Ast (1967) from Poland include *Claopodium* sp., and *Heterocladium squarrosulum*. Therefore, fossilized evidence of pleurocarpous mosses from the Miocene that today share some of the same habitats as *Lescuraea*, as well as evidence for rapid diversification of other extant taxa during this period, could support the evolution of *Lescuraea* during this time.

Lescuraea may have evolved relatively recently in Europe in the Middle Eocene (50 myr BP) to the Early Miocene (23.7 myr BP), from a common ancestor. From here, several taxa probably dispersed to eastern North America while the continents were still joined or within close proximity to one another, and formed another centre of diversity in North America. Similarly, taxa probably dispersed from Europe to northern and eastern Asia. Schofield (1968, 1969, 1976, 1980) examined the phytogeography of mosses including *Lescuraea*, focusing mostly on North America and British Columbia. The fact that bryophytes show similar disjunct patterns as angiosperms (Crum 1972, Schofield and Crum 1972, Schofield 1980), has lead some researchers to conclude that bryophytes are not subject to long-distance dispersal, despite their small diaspores. Instead, it is hypothesized that many bryophytes display a vicarious distribution. In vicariance biogeography, the distribution of organisms depends on their normal means of dispersal. Consequently, "disjunctions are explicable in terms of new barriers having split former continuous ranges, rather than in terms of the organisms hopping over already existing barriers (Allaby 1992)." These formerly continuous ranges comply with the geological dates of when each of the continents was still joined.

This chapter will attempt to show some of the major hypotheses describing the phytogeography of taxa in *Lescuraea*, with an emphasis on North America. Sixteen taxa listed from various regions of Asia and Africa by Wijk *et al*. (1964, 1967) and recognised in a checklist by Crosby *et al.* (1999) have not been examined (Table 3.3). Consequently, their status within *Lescuraea* is unclear, and they will not be discussed any further. Future completion of a monograph of *Lescuraea* will resolve the status of these taxa, which may support or add insight into the phytogeography of this group.

3.2.1. Subgenera *Lescuraea* and *Pseudoleskea*

Lescuraea has a Holarctic distribution, with several unconfirmed taxa in the Paleotropics (Fig. 3.2). This distribution represents both confirmed specimens as well as literature reports, and as such is an estimate of the extent of *Lescuraea*. Based on an examination of herbarium specimens, the confirmed distribution of *Lescuraea* is from the

Chibiny Mountains in Northern Russia, Scandinavia, Scotland, Iceland, Europe, and parts of Asia and North America. Specifically, in Europe *Lescuraea* is predominant throughout the Alps, Carpathians, Dinaric Alps, and into the Pyrenees and Cantabrian Mountains. Specimens have also been examined from Croatia, Bulgaria, Mt. Olympus, and Pindus Mountains in Greece, the Kuzey Anadolu Daglari, and Taurus Mountains in Turkey, and in the Caucasus and Ural Mountains. In Central Asia, *Lescuraea* has been collected from the Tian Shan Mountains between Kazakhstan and China, Sichuan province in China, the Kashmir region of India, and in central Nepal. In eastern Asia, *Lescuraea* has been documented from Korea, and from Ganju, Hyachine, and Hokkaido, and Honshu in Japan. Ignatov and Afonina (1992) listed taxa of *Lescuraea* in the regional divisions of the former USSR, a number of which correspond to the confirmed distribution of *Lescuraea* in the European and Far East regions. However, several collections reported from the Arctic floristic province, as well as from eastern and southern Siberia remain unconfirmed. In North America, *Lescuraea* extends from the Aleutian Islands into Alaska and down along the mountain ranges into the heart of western North America; as well as being disjunct in eastern North America in several localities of higher elevation, and in Greenland (Fig. 3.3). Therefore, a revised distribution of *Lescuraea* supports a distinctly Holarctic distribution, with the greatest diversity of taxa known from North America and from Europe (including Scandinavia) (Fig. 3.4). Fewer taxa are known from northern, central, and East Asia.

All taxa in *Lescuraea* inhabit montane to alpine slopes at elevations of 300 to 3350 metres, with the majority at elevations in excess of 1200 m. An important ecological feature distinguishing the two subgenera suggests that subgenus *Lescuraea* is somewhat more restricted in its range to far northern regions, and is found southward into warmer regions only at high elevations (Koch 1955). In the Gorce Mountains of the Polish Carpathians for example, *L. incurvata* (subg. *Pseudoleskea*) was found at elevations of 600 to 1311 m, while *L. saxicola* (subg. *Lescuraea*) was never found above 1150 m (Lisowski and Kornas 1966). In southern Europe on the other hand, both *L. saxicola* and *L. mutabilis* (subg. *Lescuraea*) are found almost exclusively above 1200 m. Taxa in both subgenera prefer a typical mountain climate of cooler and wetter conditions (Lisowski and Kornas 1966), and some like *L. radicosa* var. *compacta* (subg.

Pseudoleskea), are often found at high elevations near areas of melting snow (Lawton 1971). *Lescuraea incurvata* and *L. radicosa* var. *compacta* are known from elevations of 500 to 3000 m and above 1500 m respectively, in the Pacific Northwest; reaching their highest elevations in Nevada, Utah, and Colorado (Lawton 1971). Along the Coast and Cascade Mountains of North America, the endemic taxon *L. atricha* (subg. *Pseudoleskea*) prefers elevations of 1600 to 2200 m.

Habitat preferences of *Lescuraea* include upper montane forests to alpine tundra, where taxa are predominantly saxicolous or corticolous in the former zone, to saxicolous or even terricolous in the latter zone. Substrate preferences for most taxa include siliceous rocks (igneous, gneiss, quartzite), with some taxa collected from calcareous rocks. For example, *L. atricha*, *L. incurvata* var. *incurvata*, *L. patens* (subg. *Pseudoleskea*), *L. radicosa* var. *radicosa* (subg. *Pseudoleskea*), *L. radicosa* var. *compacta*, and *L.saxicola* are primarily found on siliceous rocks, while *L. incurvata* var. *tenuiretis* (subg. *Pseudoleskea*) is found principally on calcareous rocks. Corticolous taxa *L. saviana* and *L. stenophylla* (both subg. *Pseudoleskea*) are restricted to buttresses of trees, and stems and branches of shrubs respectively (Schofield 1976). Most taxa of *Lescuraea* are only rarely terricolous. However, *L. radicosa* var. *denudata* (subg. *Pseudoleskea*) is found almost exclusively on soil among heath and grasses in alpine meadows.

In the Gorce Mountains of the Polish Carpathians, Lisowski and Kornas (1966) determined that taxa in *Lescuraea* were restricted to the western region of the range where there were numerous acidic rock outcrops, higher elevations, and increased precipitation. In the eastern region of the range, proximity to the calcareous Pieniny Range results in soils high in calcium carbonate. In addition, there is reduced precipitation and increased temperature in the eastern region of the range due to a lower elevation (Lisowski and Kornas 1966). Although never addressed by Lisowski and Kornas (1966), the occurrence of *L. incurvata* var. *tenuiretis* in predominantly calcareous regions of western North America and Europe, may be a result of the limitation of this taxon to compete with other species on siliceous substrates. On the other hand, the extremely compact and stiff habit of this taxon may also suggest desiccation tolerance, and thus niche exploitation.

3.2.2. Endemism

The majority of taxa in *Lescuraea* display disjunct distribution patterns. However, two endemics have been confirmed from North America and a single taxon is endemic to Europe.

North America

According to Schofield (1968) and Lawton (1971), and confirmed here, *Lescuraea atricha* and *L. incurvata* var. *gigantea* are endemic to North America in the western mountainous region of the continent. Lawton (1971) also included *L. incurvata* var. *tenuiretis* as a third endemic to western North America. However, specimens examined in the revision clearly support the presence of this taxon in Europe. *Lescuraea atricha* and *L. incurvata* var. *gigantea* occur exclusively west of the Rocky Mountains, with several confirmed collections of the former taxon in a few localities along the western slopes of the Rockies. This taxon has not been confirmed from the eastern slopes of the Rocky Mountains. In the montane conifer forest, a related species, *Rigodiadelphus baileyi*, is known from the Insular, Cascade, and Coast Mountains, sometimes extending into the adjacent foothills. This taxon is endemic to North America, as well as being the sole representative of *Rigodiadelphus* in North America. *Rigodiadelphus baileyi* prefers elevations between 425 to 1000 metres. However, it is also known from very low elevations throughout Alaska (Lawton 1971). Since the Coast Mountains were formed in the Pliocene (13-2 myr BP), both *Lescuraea atricha* and *Rigodiadelphus bailey* may have evolved at this time, with present-day distributions possibly reflecting a more recent (e.g., Pleistocene epoch) vicariance event.

During the Pleistocene, the Rocky Mountains of Canada and regions farther west were engulfed in the Cordilleran Ice Sheet, while most of Canada and parts of the United States east of the Rockies, were covered by the Laurentide Ice Sheet. This resulted in the separation of the flora and fauna of the East from the West. As such, many species of plants and animals are found on only one side of the Continental Divide (Elias 1996). Schofield (1980) proposed that some of the bryoflora of western North America survived the glaciations south of the glacial boundaries in the western United States. This assumption is supported by the presence of a subfossil record of southwestern British Columbia (Mathewes 1973) containing a number of endemics such as *Isothecium* *stoloniferum*, *Dendroalsia abietina*, and *Leucolepis menziesii* that were presumably growing there while glaciers were still present in the adjacent highlands (Schofield 1980). Unfortunately, there are no known fossils of *Lescuraea*, so it is unclear if they also survived the glaciations south of the glacial boundary and migrated northward after deglaciation, or if they are the outcome of relatively recent speciation events. Specifically, if *L. atricha* evolved in the Pliocene along the Cascade and Coast Mountains, then this taxon may have survived the glaciations south of the glacial boundary. Recent migration northward after glacial retreat may explain its range expansion to several localities on the west slopes of the Canadian Rockies. Conversely, *L. atricha* may have evolved in the Coast region long after deglaciation, indicating recent and thus limited expansion eastward. However, since all other North American taxa in *Lescuraea* (except *L. incurvata* var. *gigantea*) are also found throughout the Rocky Mountains, on both sides of the Continental Divide, recent speciation seems a likely possibility for *L. atricha*.

Europe

Lescuraea mutabilis is a confirmed endemic to Europe, while *L. glacialis* is an unconfirmed taxon, requiring examination. *Lescuraea mutabilis* is restricted to 'Krummholz' *Fagus sylvatica* and *Rhododendron hirsutum* stems and twigs, and is predominant in the Alps, Black Forest, and in the Dinaric Alps. *Lescuraea mutabilis* is gametophytically and in part sporophytically very similar to *L. saxicola*. As a result, it is hypothesized that the former evolved from a common ancestor with the latter taxon, as plants became epiphytic. Another epiphyte (*L. saviana*), although not endemic, is common in southern Europe and rare in western North America. While this taxon grows on trunks of *Fagus sylvatica* in montane to subalpine regions in southern Europe, it tends to be saxicolous or rarely corticolous and found on smaller twigs in western North America.

3.2.3. Disjunctions

Although endemics have specific patterns of occurrence, a greater proportion of taxa show a broad distribution pattern. *Lescuraea radicosa* var. *radicosa*, *L. incurvata* var. *incurvata*, *L. patens*, and *L. saxicola* are known from many localities throughout the generic distribution, while *L. stenophylla*, *L. saviana*, *L. radicosa* var. *compacata*, *L. radicosa* var. *denudata*, *L. incurvata* var. *tenuiretis*, and *L. incurvata* var. *gigantea* have more restricted distributions (Fig. 3.5). It is possible that the former four taxa evolved in Europe in the Middle Eocene (50 myr BP) to the Early Miocene (23.7 myr BP), dispersing to Asia and North America shortly thereafter, forming a continuous circumboreal distribution. The lack of taxa in *Lescuraea* in comparable habitats in Southeast Asia and in Australasia can be explained by the fact that these landmasses were joined with Antarctica until the Middle Eocene, and did not approach East Asia until the Middle Miocene (13-2 myr BP) (Brown and Lomolino 1998). If these taxa evolved in the Middle Eocene and diversified shortly thereafter, this would explain why they could not have reached Southeast Asia or Australia. Similarly, early separation of South America from Africa in the Late Jurassic (152 myr BP) to the Early Cretaceous (120 myr BP) supports the absence of *Lescuraea* from other continents of Gondwanan origin. Even if *Lescuraea* evolved in the Cretaceous (≈100 myr BP), corresponding to the last direct overland migration possible between South America and Africa (Raven and Axelrod 1974), climatic changes over the last 60 million years would have "decimated the African populations" (Miller 1982). However, given that there is no known distribution of *Lescuraea* in South America, not even in the subalpine or alpine zones of the Andes, this supports the hypothesis that *Lescuraea* evolved some time after the separation of Gondwanaland.

Although there is abundant information concerning western North American – western European – western Asian– eastern Asian disjunctions (Raven and Axelrod 1974), Raven (1963) suggested that a great majority of angiosperms reached their areas of disjunction by long-distance dispersal. Since moss spores are so much smaller than spores of angiosperms, documentation of *Lescuraea* in these regions could be explained by this method. From experiments conducted on long-range dispersal of bryophyte spores, Van Zanten (1978*a*, 1978*b*, 1984) determined that moss spores of temperate species could survive desiccation periods of between six months to three years or more, while moss spores of moist tropical taxa had limited tolerance. Van Zanten (1984) suggested that moss spores are resistant to wet-freezing episodes in the jet stream to a certain degree, although they do have higher "fatality rates" than dry-frozen spores. Van

Zanten (1978*a*, 1978*b*, 1984) concluded that temperate moss species have the greatest potential for "effective, intercontinental long-distance dispersal via dry air-streams either at relatively low altitudes or at high altitudes (jet-streams) or both (Van Zanten 1984)." Since *Lescuraea* inhabits moist microhabitats in high-elevated mountains, they may in fact be tolerant to very cold moist conditions, and thus their spores may survive wet-freezing episodes in the jet stream. Consequently, if long-distance dispersal of spores is a possibility for *Lescuraea*, this may explain some of the disjunctions observed. However, it is just as likely spores of *Lescuraea* have a high "fatality rate" in the jet stream, and do not readily become established (Van Zanten 1984). The absence of *Lescuraea* from comparable habitats in other parts of the world (e.g., the Andes) could potentially be explained by an inability of spores to survive long-distance dispersal or due to establishment limitations.

It is important to indicate that all taxa in *Lescuraea* are dioicous, and as such, sporophyte production (giving rise to spores) is often at a minimum, especially in alpine regions. Both male and female plants must be within a few centimetres of each other in order for the biflagellate motile sperm to reach the archegonium and fertilize the egg. If male and female plants are not within close proximity to one another, they must find other means of reproduction. No vegetative diaspores have ever been seen on any *Lescuraea*. However, absence of gemmiparous structures on many dioicous mosses (Miller 1982) including *Lescuraea* does not negate the dispersal of gametophytes over considerable distances. The fragile nature of plants during normal dry phases of growth results in fragmentation at exactly those times when maximum opportunities for transport exist. Fragments are viable so long as survival tolerance limits are not exceeded. As a result, "any living bryophyte cell has the potential to establish a new plant and normally will do so in an amenable niche (Miller 1982)." According to Miller (1982), deciduous branchlets and variously derived fragments are of great importance for localized dissemination, with medium to long dispersal being accomplished in several cases. Although not verified in *Lescuraea*, branchlets and fragments may be responsible for localized dissemination.

Laurasian distribution

There are a number of species of bryophytes, such as *Lescuraea radicosa* var. *radicosa*, *L. incurvata* var. *incurvata*, *L. patens*, and *L. saxicola* that show disjunct distribution patterns between western and eastern North America, Western Europe, and western and eastern Asia. Absence of these disjunct taxa from most of Asia, with the exception of parts of Siberia, the Himalayas, the Ural and Tian Shan Mountains, and the easternmost region, may also imply that they have been isolated for many thousands of years at least. If this hypothesis is valid, many taxa could have had wider ranges in the past, perhaps as remnants of a circumboreal flora from the late Pliocene (5.3-1.9 myr BP) (Schofield 1969, 1980). That much of the western North American flora is a fragment of a more widespread flora of Eurasian origin appears indisputable (Schofield 1969). Schofield (1980) hypothesized that climatic and vegetation changes reduced the once much larger range to its present form. This hypothesis is supported by a study performed in northwest North America, where pollen data records have shown that local vegetation changes during the past 125 kyr were controlled by global variations in the climate system (Whitlock and Bartlein 1997). Among these controls were millennial-scale variations in the seasonal cycle of insolation and size of the ice sheet, which affected regional climates directly through changes in temperature and net radiation, and indirectly by shifting atmospheric circulation. According to Whitlock and Bartlein (1997), "species kept pace with millennial-scale climate changes by expanding their ranges short distances from discontinuous refugia." As a result, periods of low ice volume and summer insolation maxima featured xerothermic taxa, while periods of moderate ice volume and summer insolation minima supported subalpine conifers. During the last half of the previous interglaciation (≈ 133-116.7 kyr BP), summer insolation exceeded that of the early Holocene (≈ 13 kyr BP) and global ice volume was at its lowest. These conditions fostered a warm, dry climate and an expansion of xerophytic forest (*Pinus ponderosa*, *P. contorta*, *Quercus* sp.) and steppe elements. While cooler than present conditions, the period from ≈ 117-83 kyr BP, and in the early to middle Wisconsin interval (73.9-27.6 kyr BP), supported mixed conifer forests of *Pinus* sp. and *Picea* sp. (Whitlock and Bartlein 1997). Similarly, Elias (1996) indicated that during the late Pleistocene, both latitudinal and altitudinal zones of the Rocky

Mountains were pushed southward and down-slope respectively. As a result, Arctic tundra became established south of the continental ice sheet in the Midwestern United States, Boreal forests grew south of the tundra zone, and in the Rockies, the boundary between alpine tundra and subalpine forest pushed down-slope hundreds of metres. In some places, coniferous forests even expanded their ranges out onto the Plains (Elias 1996).

Lescuraea has very specific habitat and ecological requirements, being restricted for the most part to acidic rock and tree bark in montane to alpine zones of moist mountain slopes. If *Lescuraea* is most competitive at higher elevations, then its absence in the low-lying central region of North America, where competition from other species is greatest, appears logical. However, the fact that many taxa have not extended their range across North America today could also be climatically related. If in the Tertiary (64-2 myr BP), the central region of North America was cool and moist enough to support a cordilleran flora in the temperate forests, it is at present too warm and dry to support such a flora. These taxa may have thrived in a continuous zone at lower elevations in the past, and migrated up-slope relatively recently to seek moist and cool habitats.

The importance of *L. stenophylla* and several other taxa in the ecology of local vegetation is shown in that there are many other species that could occupy habitats in these areas, but they are not equally competitive (Schofield 1980). According to Szweykowski (1984), many mosses grow in rather stable habitats, such as on rocks at high mountain elevations. These and other sites are very similar in that they have the characteristics of early succession stages. Thus the "problem of competition with higher plants is not relevant here, the ability to endure being the most essential requirement" (Szweykowski 1984). These habitats are ecologically relatively stable during the life cycle of the bryophyte. However, optimal conditions for vegetative growth of gametophytes can differ considerably from those that are optimal for the production of sporophytes. It is well known that when gametophytes grow luxuriantly, they are usually sterile or produce only gemmae, and that gametangia and sporophytes are only produced when conditions of growth deteriorate (Szweykowski 1984). In the case of *Lescuraea, L. radicosa* var. *denudata* is exclusive to alpine meadows and tundra in North America and in Europe, where it is terricolous and found growing under a protective canopy of heath plants. This very large and robust taxon forms extensive wefts and dominates the alpine soil, producing very few branches, and produces sporophytes only in extreme cases. As a result, it seems likely that this taxon dominates this habitat through continued growth of the gametophyte, or from vegetative fragments of branches.

Although the possibility that *Lescuraea* displayed a circumboreal distribution in the past is compelling, the presence of *L. radicosa* var. *radicosa*, *L. incurvata* var. *incurvata*, *L. patens*, and *L. saxicola* in northern, central, and eastern Asia may also be a function of long-distance dispersal of diaspores. According to Van Zanten (1978*a*, 1978*b*, 1984), temperate moss species have the greatest potential for "effective, intercontinental long-distance dispersal via dry air-streams either at relatively low altitudes or at high altitudes (jet-streams) or both (Van Zanten 1984)." Nonetheless, the absence of *Lescuraea* in comparable habitats in other regions of the world (e.g., Andes) suggests perhaps that long-distance dispersal of diaspores is unlikely, or that establishment is somehow inhibited. The fact that all taxa of *Lescuraea* produce sporophytes in all regions of their distribution indicates that both male and female plants occur throughout their range. If long-distance dispersal of spores were a factor, one should expect to see some taxa that are strictly male or female (and as such do not produce sporophytes) in parts of their range. However, the presence of sporophytes in all taxa supports that *Lescuraea* once displayed a more circumboreal distribution that has since been affected by vicariance events (e.g., plate tectonics, orogeny etc.).

Isolation of *Lescuraea saxicola* populations on mountain slopes over thousands of years has lead to subtle gametophytic differences. The most striking example of this is where European, Japanese, and North American plants of *L. saxicola* differ somewhat in the shape and number of paraphyllia present. In contrast to the numerous, large, and lanceolate paraphyllia of European and most North American plants, those of Japan and northwest North America are few, small, and filamentous. Frequently, paraphyllia are nearly lacking in Japanese plants (Noguchi 1972). The isolation of other taxa in *Lescuraea* to specific habitats on mountain slopes for many thousands of years may have led to relatively recent speciation events and thus endemism in specific areas.

Bicentric distribution

Belland and Schofield (1988) collected specimens of *Lescuraea stenophylla* from Cape Breton Island, Nova Scotia, which had not been previously documented from eastern North America. My revision has revealed that part of the problem lay in misidentification of specimens. Currently, the distribution of *L. stenophylla* reveals numerous collections from Gaspé, Quebec as well as from Newfoundland. The presence of this species in eastern North America does not appear to be coincidental, but "disjuncts of this type form a much larger group of eastern North American – western North American disjunct mosses" (Belland 1987*a,b*, Belland and Schofield 1988). Belland and Schofield (1988) proposed that *L. stenophylla* could have occupied a much larger range in North America before glaciation, where the general cooling trend during the Tertiary allowed the expansion of this cordilleran species to the temperate forests of eastern North America. On the other hand, Belland and Schofield (1988) also suggested that the presence of *L. stenophylla* in eastern North America might have been the result of small disjunct ranges that existed before glaciation and persisted in unglaciated refugia. Long-distance dispersal as a means of explaining this disjunction does not seem probable (Belland and Schofield 1988).

Other predominantly cordilleran taxa displaying more northern distributions in North America, but also showing wide disjunctions in eastern North America are: *Lescuraea radicosa* var. *radicosa* (Belland and Schofield 1988), *L. radicosa* var. *compacta*, *L. patens*, *L. incurvata* var. *incurvata*, and *L. saxicola*. Taxa showing tricentric distributions, occurring in the east as well as in the Great Lakes region are *L. radicosa* var. *radicosa* (Belland and Schofield 1988), *L. patens* (Ireland 1982), and *L. incurvata* var. *incurvata* (Fig. 3.5). Crum (1997) indicated that *L. saxicola* occupied a non-continuous range at northern latitudes, and was known in Michigan from a single locality near Copper Harbour, in Keweenaw County. Although Crum (1997) indicated that Fred Hermann collected this specimen in 1960, he neglected to include either a collection number or herbarium accession number. Hermann's specimen was unavailable for review, and as such, Crum's findings cannot be verified here. However, the possibility that the Keweenaw Peninsula, as well as other elevated areas along the northern and southern shores of Lake Superior (e.g., Huron Mountains) may have escaped glaciation is evident in the presence of a number of other cordilleran species there (Steere 1937). It has been suggested by Schofield (1969), Crum (1972), and Belland and Schofield (1988) that the species in the St. Lawrence region survived in refugia, while species in the Great Lakes region are a result of postglacial migration from areas to the south.

Amphi-Pacific distribution

According to Schofield (1968, 1980), *Lescuraea julacea* (= *L. saxicola*) displays an Amphi-Pacific disjunction between coastal regions of the northwestern United States, British Columbia, Alaska, and along the Aleutian Islands into Japan. Schofield (1969) concluded that this species originated in eastern Asia, and like other species, did not expand its range via the Bering Land Bridge, but rather along the chain formed by the Aleutian Islands. Noguchi (1972) and Noguchi *et al.* (1991) synonymized *L. julacea* with *L. saxicola*, which is supported in my revision. As described earlier, *L. saxicola* has a western North American – eastern North American – western European – western and eastern Asian disjunction. *Lescuraea saxicola* may have had a continuous distribution when the continents of Laurasia were still joined. When Europe and North America had separated more than 40 myr BP, so that short-distance dispersal was no longer possible between them, isolated East Asian populations of *L. saxicola* may have evolved subtle changes in paraphyllia size and frequency, differentiating them from what some believe to be a valid species *L. julacea*. Then as the Aleutian Islands became available in the late Pleistocene, migration into western North America became possible.

If *Lescuraea saxicola* evolved in eastern Asia and then migrated across the Aleutian Islands into North America during the late Pleistocene, as suggested by Schofield (1968, 1980), then it is also a plausible explanation for the distribution of the North American taxon *Rigodiadelphus baileyi*. *Rigodiadelphus* displays an Amphi-Pacific distribution (Fig. 3.6), with *R. robustus* endemic to Japan, Korea, and Sakhalin Island in Russia, *R. arcuata*, endemic to Honshu, Japan, and *R. baileyi* endemic to the coastal regions of western North America. Ignatov and Afonina (1992) provided a general distribution for *Rigodiadelphus* in the former USSR, revealing that this genus is limited to the southern portion of the Far East. Unfortunately, no information pertaining to the possible distribution of *Rigodiadelphus* in Northeastern Russia was reviewed. As a result, it is unknown whether Asian and North American populations have a parapatric distribution in this area. However, it is hypothesized that during the late Pleistocene, *R. robustus* traversed across the Aleutian Islands from Japan, making its way into Alaska and down along the West Coast of North America.

According to Pielou (1991), most of Asia, Russia, and Northwestern Alaska were ice-free during the Pleistocene. At the same time as taxa were migrating across the Aleutian Islands, or probably sometime later, the East Asian plants of *Rigodiadelphus robustus* developed a reduced peristome, believed to have evolved as a result of having become epiphytic. In comparison, *R. baileyi* has an unreduced hypnobryalean peristome, is terricolous and saxicolous in Alaska, and is often corticolous in southern British Columbia, Washington, and Oregon. Lawton (1957) revealed that the peristome of this taxon is irregular in shape and size, showing a reduction trend of the peristome typical of epiphytic habitats. Unfortunately, this observation was not confirmed here. However, if *R. baileyi* becomes increasingly epiphytic in the future, it is hypothesized that the peristome will also become reduced, possibly resembling the peristome of *R. robustus*. A phylogenetic analysis from a variety of methods (e.g., morphological, molecular) may help support the hypothesis that *R. arcuata*, *R. robustus*, and *R. baileyi* are closely related, and as a result help support their origin and distribution as a genus.

3.2.4. Centres of Diversity

Cain (1944) outlined the thirteen criteria used and abused for indicating the centre of origin of a taxon, suggesting that none of them could reliably identify the centre of origin of a group. Where some authors chose the centre of origin based on the location of the greatest differentiation of a type, others based the origin on the location of taxa with the most primitive characters. In the latter tenet, speciation occurs in the periphery of the range. However, Cain (1944) cautioned against following this tenet exclusively since taxa with primitive characters often survived in isolated regions (relicts) containing few competing species and located far from their original ranges. Since the location of the centre of origin for *Lescuraea* cannot be supported without a fossil record or a phylogenetic analysis of the taxa, the following discussion will focus on the centres of diversity of *Lescuraea*.

While there is no literature pertaining solely to the phytogeography of *Lescuraea*, it appears that the centres of diversity for *Lescuraea* are in western North America and in Europe (Fig. 3.4). If a taxonomic study supports the inclusion of the presently unconfirmed African and Asian species within *Lescuraea* (Table 3.3), this may support secondary centres of diversity.

Based on the centres of diversity, some hypotheses of the evolution of *Lescuraea* are proposed. *Lescuraea* may have evolved in Europe when the continents of Laurasia were still joined, with the common ancestors of *L. radicosa*, *L. incurvata*, *L. patens*, and *L. saxicola* dispersing to eastern North America and across the continent to the west, and westward across Asia from Europe; thereby forming a continuous distribution. Subsequent speciation may explain the current distributions of *L. stenophylla*, *L. saviana*, *L. incurvata* var. *gigantea*, *L. atricha*, and *L. mutabilis*. While *Lescuraea stenophylla* is an epiphyte common in western North America, it is both rare in eastern North America and in western Europe. This species may have evolved in western North America along the newly formed Rocky Mountains and dispersed eastward into suitable habitats, including several populations in Europe, before North America and Europe began to separate approximately 40 myr BP. Conversely, *Lescuraea saviana* is an epiphyte common in southern Europe, yet rare in western North America and not present in eastern North America. This taxon may have evolved in Europe at the same time as *L. stenophylla*, dispersed to North America, and subsequently went extinct in eastern North America, possibly during the Pleistocene epoch. The evolution of *L. incurvata* var. *gigantea*, *L. atricha*, and *L. mutabilis* is hypothesized to have occurred long after North America and Europe separated 40 myr BP, probably sometime during the Pliocene (13-2 myr BP). Both *L. incurvata* var. *gigantea* and *L. atricha* are endemic to western North America, west of the Continental Divide, while *L. mutabilis* is endemic to Europe.

3.2.5. Conclusion

The genus *Lescuraea* may have evolved relatively recently in Europe in the Middle Eocene (50 myr BP) to the Early Miocene (23.7 myr BP), dispersing to North America and to Asia, with subsequent speciation occurring in both western North America and in Europe, resulting in two centres of diversity.

Bryophytes show similar disjunct patterns to angiosperms (Schofield and Crum 1972, Schofield 1980), leading some researchers to conclude that bryophytes are not subject to long-distance dispersal, despite their small spores. However, the fact that the proportion of North American and other bryophyte endemics are much smaller than the proportion of angiosperm endemics, and that a high proportion of mosses have very wide or sometimes narrow ranges, suggests that bryophytes are indeed more prone to long-distance dispersal than angiosperms (Schofield 1980). Although this may explain the existence of some taxa in specific areas, the distribution of species that only infrequently produce spores, or where long-distance dispersal does not seem feasible, cannot be explained by this method (Schofield 1969). Instead, many species may rely on vegetative fragmentation as a means of expanding their ranges. In addition, past climate change may have reduced a more circumboreal distribution.

Since all taxa in *Lescuraea* are dioicous, selection pressures could restrict their current range to moist and cool, montane to alpine slopes of the various mountain ranges of the world, where in the past they may have had a more continuous distribution. Consequently, taxa in *Lescuraea* may have held out in microhabitats as relict populations during major climatic changes, and then expanded their ranges again afterward. This hypothesis seems likely in light of the fact that all taxa in *Lescuraea* produce sporophytes, suggesting that vicariance and not long-distance dispersal of spores is responsible for this distribution.

The proposed hypotheses attempt to explain the distribution and diversity of *Lescuraea*. However, fossil evidence or a phylogenetic analysis would clearly help support or refute some of these hypotheses.

Table 3.1. Historical classification of *Lescuraea* and *Pseudoleskea* – in sequential order within publication.

Best 1900	**Brotherus 1907 & 1925**	**Lawton 1957**
Pseudoleskea Bruch & Schimp.	*Lescuraea* Bruch & Schimp.	Lescuraea Bruch & Schimp.
in B.S.G.	*in* B.S.G.	*in* B.S.G.
	L. striata	
Subgenus *Eu-Pseudoleskea*	*L. saxicola*	**Subgenus** *Pseudoleskea*
P. atrovirens	*L. substriata*	*L. patens*
P. oligoclada	*L. julacea*	*L. incurvata*
P. pallida		*L. incurvata var. gigantea*
P. pallida var. filescens	*Pseudoleskea* Bruch & Schimp.	*L. incurvata var. tenuiretis*
	in B.S.G.	*L. saviana*
Subgenus *Radicosella*		*L. radicosa*
P. denudata	**Section** *Pseudo-Pterogonium*	*L. radicosa var. radicosa*
P. denudata var. holzingeri	*P. imbricata*	*f. jemtlandica*
P. radicosa	*P. claviramea*	*L. radicosa var. radicosa*
P. radicosa var. compacta	*P. Leikipiae*	*f. bernardensis*
P. rigescens	*P. obtusciscula*	*L. radicosa var. radicosa*
P. rigescens var. howei	*P. Artariae*	*f. holzingeri*
	P. laevissima	*L. radicosa var. denudata*
Subgenus *Lescuraea*	*P. pseudo-attenuata*	*L. radicosa var. compacta*
P. substriata	*P. leskeoides*	*L. radicosa var. pallida*
	P. Macowaniana	*L. atricha*
	P. capilliramea	*L. stenophylla*
		L. plicata
	Section *Eu-Pseudoleskea*	
	P. andina	**Subgenus** *Tricholeskea*
	P. patens	*L. baileyi*
	P. filamentosa	
	P. oligoclada	**Subgenus** *Lescuraea*
	P. pallida	*L. striata*
	P. laevifolia	*L. saxicola*
	P. papillarioides	*L. iliamniana*
	P. dispersa	
	P. peraldierii	
	Section *Orthotheciella*	
	P. chalaroclada	
	P. desmioclada	
	P. austro-catenulata	
	P. filum	
	P. lurida	
	P. fuegiana	
	P. calochroa	
	P. sordidoviridis	
	P. strictula	
	P. platyphulla	
	P. antarctica	

Table 3.2. Proposed infrageneric classification of the genus *Lescuraea* – taxa listed alphabetically.

Lescuraea Bruch & Schimp. *in* B.S.G.

- **Subgenus** *Lescuraea* (Bruch & Schimp. *in* B.S.G.) E. Lawton
  - *L. mutabilis* (Brid.) Hagen
  - *L. saxicola* (Bruch & Schimp. *in* B.S.G.) Molendo *in* Lorentz
- **Subgenus** *Pseudoleskea* (Bruch & Schimp. *in* B.S.G.) E. Lawton
  - *L. atricha* (Kindb. *In* Macoun) E. Lawton
  - *L. incurvata* (Hedw.) E. Lawton
    - *L. incurvata* var. *gigantea* E. Lawton
    - *L. incurvata* var. *tenuiretis* (Culm.) E. Lawton
  - *L. patens* (Lindb.) Arn. & C. Jens.
  - *L. radicosa* (Mitt.) E. Lawton
    - *L. radicosa* var. *compacta* (Best) E. Lawton
    - *L. radicosa* var. *denudata* (Kindb. *in* Macoun & Kindb.) E. Lawton
  - *L. saviana* (DeNot.) E. Lawton
  - *L. stenophylla* (Ren. & Card.) E. Lawton

Table 3.3. Taxa in *Lescuraea* with unconfirmed status. These species are listed in Crosby *et al*. (1999) as *Lescuraea* and *Pseudoleskea*.

Lescuraea	***Pseudoleskea***
L. glacialis Amann	*P. attenuata* Brotherus & Paris
L. longipes Brotherus & Paris	*P. coreana* Uno & E. Takahasi
L. secunda Arnell	*P. dispersa* C. Müller
	P. korjakorum Lazarenko
	P. laevissima Cardot
	P. leikipiae (C. Müller) Paris
	P. penzigii Brizi
	P. perraldieri Bescherelle
	P. plagiostoma C. Müller
	P. pseudoattenuata (C. Müller) Brotherus
	P. semensis (C. Müller *in* Venturi) Jaeger
	P. tonkinensis Bescherelle
	P. trichodes Bescherelle

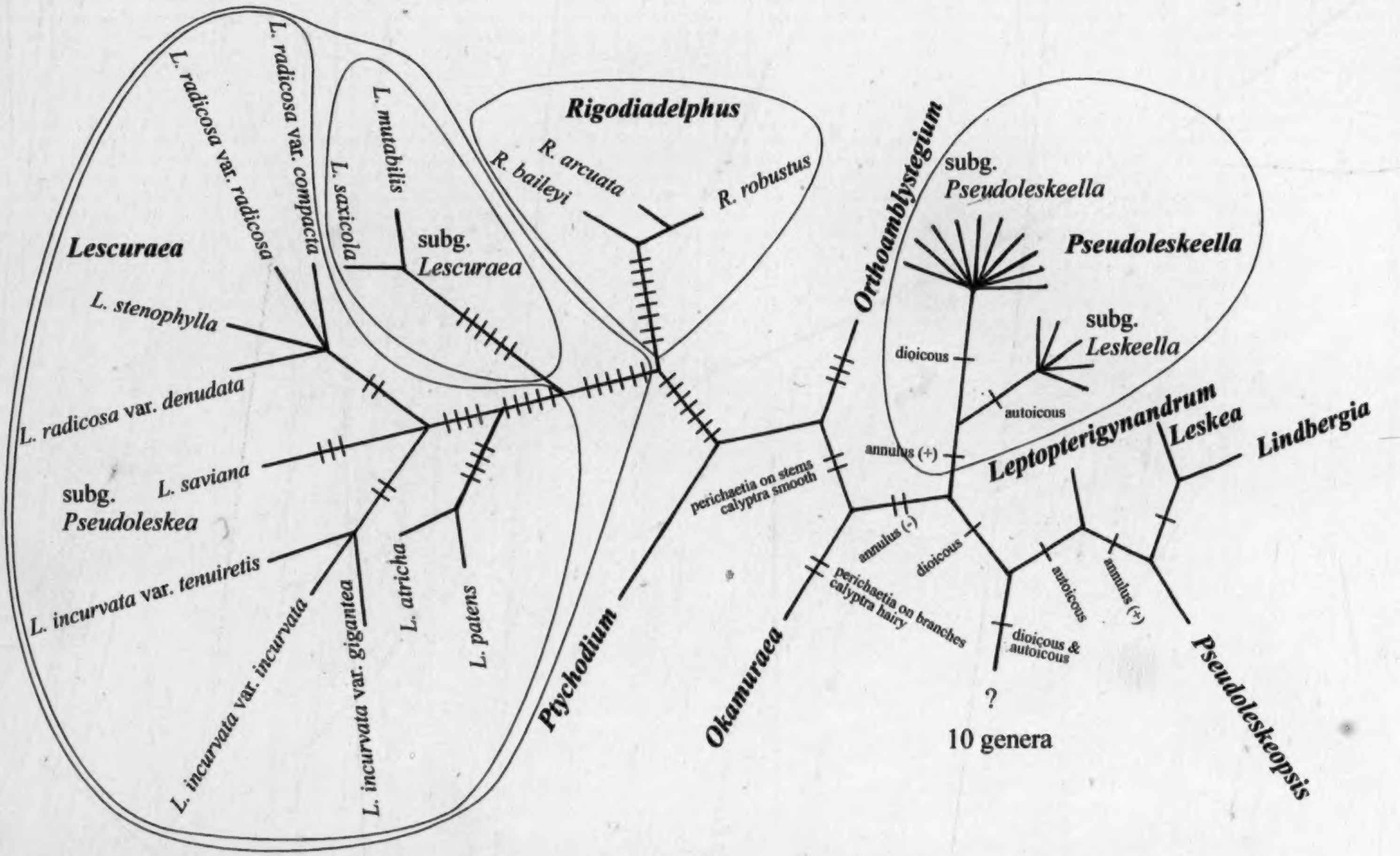

Lescuraea
L. radicosa var. radicosa
L. radicosa var. compacta
L. stenophylla
L. radicosa var. denudata
L. mutabilis
L. saxicola
subg. Lescuraea
subg. Pseudoleskea
L. saviana
L. incurvata var. tenuiretis
L. incurvata var. incurvata
L. incurvata var. gigantea
L. atricha
L. patens
Rigodiadelphus
R. arcuata
R. baileyi
R. robustus
Ptychodium
Orthoamblystegium
perichaetia on stems
calyptra smooth
Okamuraea
perichaetia on branches
calyptra hairy
annulus (-)
subg. Pseudoleskeella
Pseudoleskeella
subg. Leskeella
dioicous
autoicous
annulus (+)
Leptopterigynandrum
Leskea
Lindbergia
dioicous
autoicous
annulus (+)
dioicous & autoicous
?
10 genera
Pseudoleskeopsis

Figure 3.1. Unrooted tree displaying hypothesized relationships among the Leskeaceaea. Characters defining groups are indicated by bars. Not all characters are depicted.

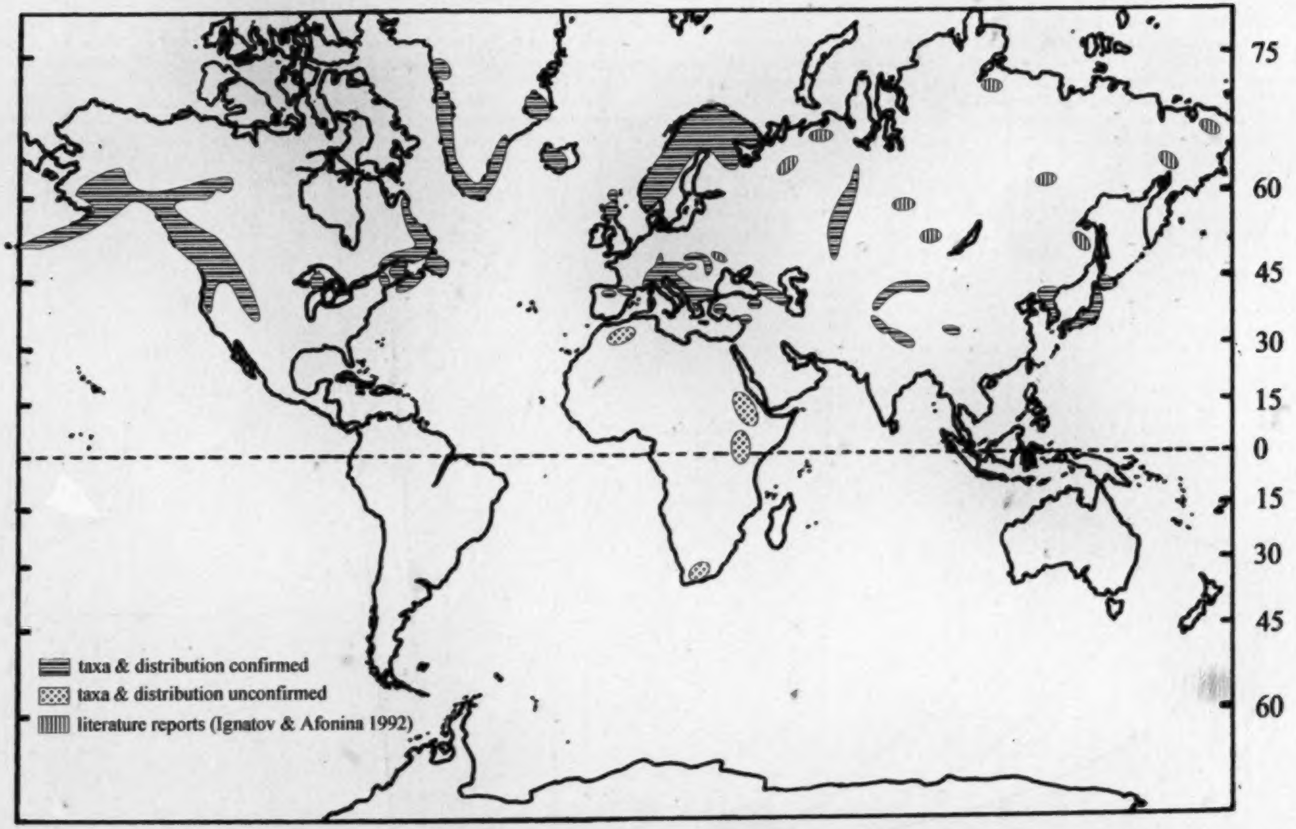

75
60
45
30
15
0
15
30
45
60
▤ taxa & distribution confirmed
▩ taxa & distribution unconfirmed
▥ literature reports (Ignatov & Afonina 1992)

Figure 3.2. Global distribution of *Lescuraea.* Examined specimens represented by horizontal line pattern. Unexamined specimens represented by dotted and vertical line patterns.

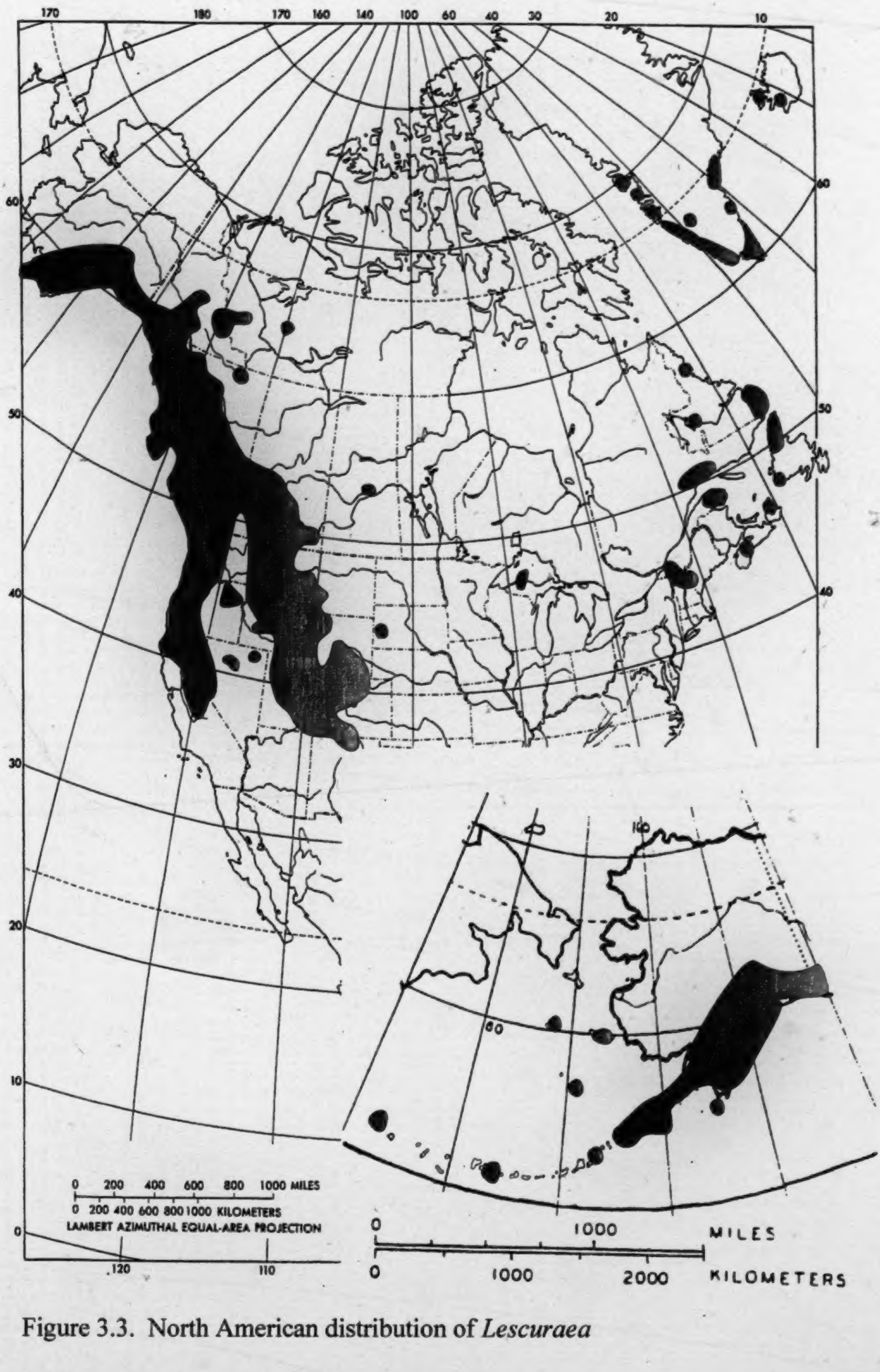

170
180
170
160
140
100
60
40
30
20
10
60
50
40
30
20
10
0
0 200 400 600 800 1000 MILES
0 200 400 600 800 1000 KILOMETERS
LAMBERT AZIMUTHAL EQUAL-AREA PROJECTION
120
110
160
60
0
1000
MILES
0
1000
2000
KILOMETERS

Figure 3.3. North American distribution of *Lescuraea*

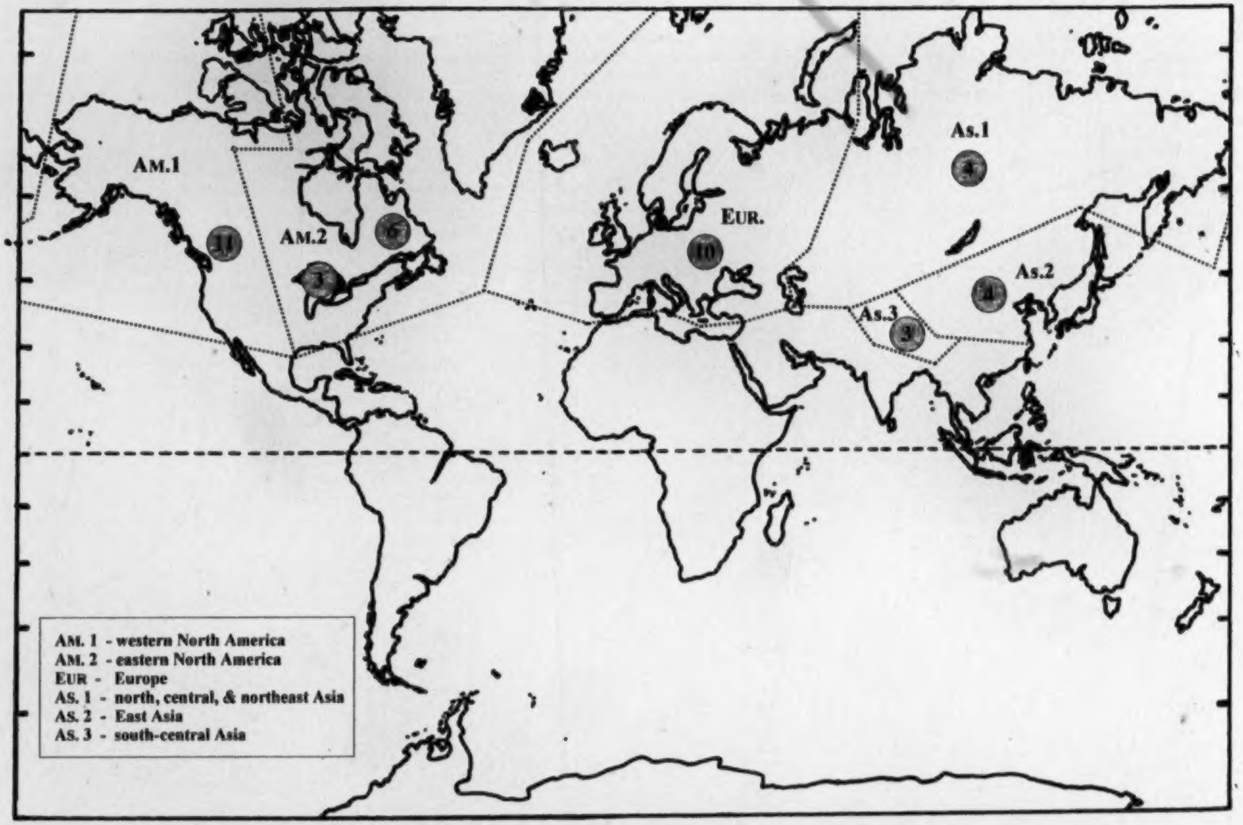
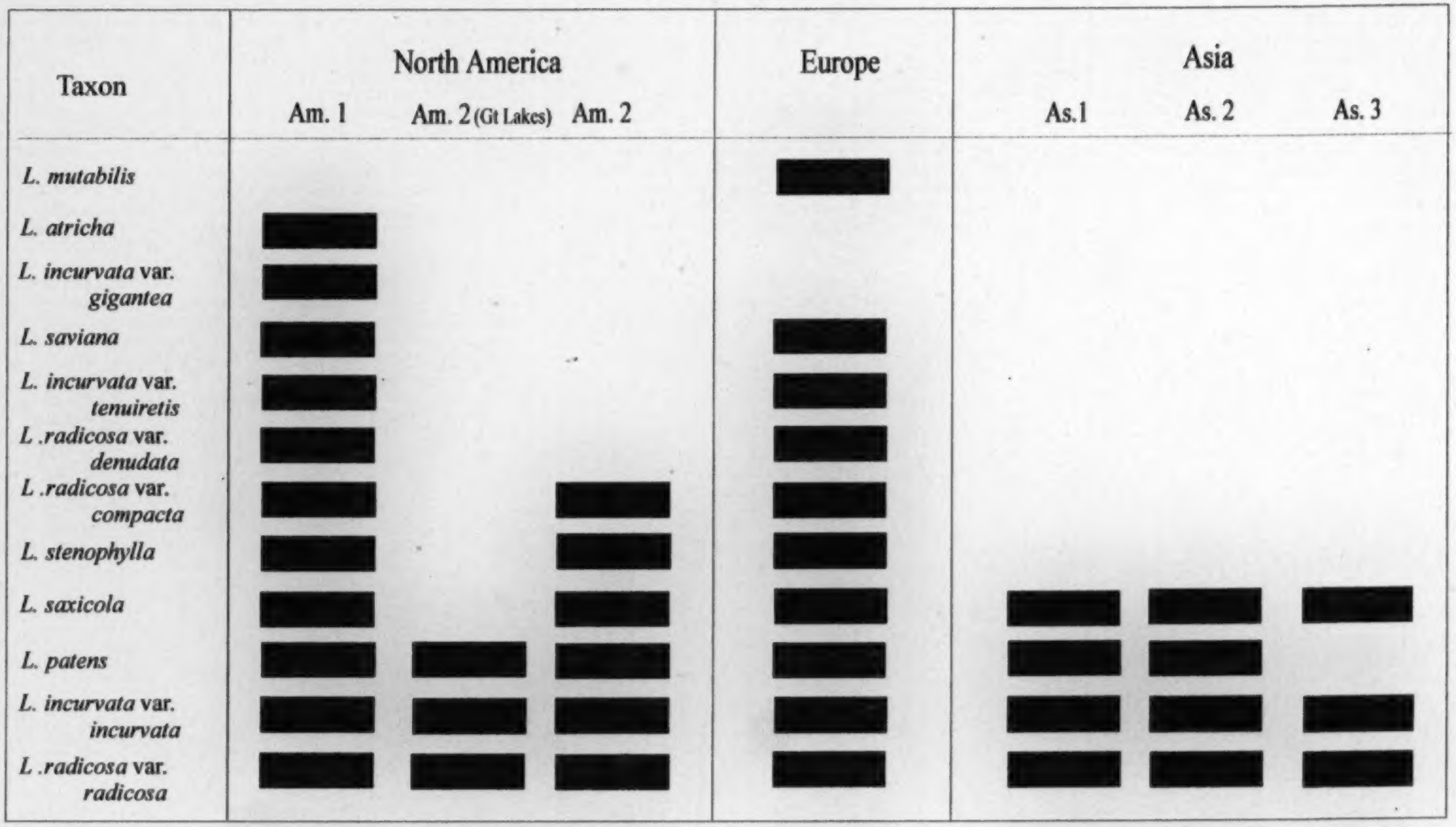

AM.1
11
AM.2
6
3
EUR.
10
As.1
4
As.2
4
As.3
3
AM. 1 - western North America
AM. 2 - eastern North America
EUR - Europe
AS. 1 - north, central, & northeast Asia
AS. 2 - East Asia
AS. 3 - south-central Asia

Figure 3.4. Global diversity of *Lescuraea.* Circles indicate confirmed number of taxa in a generalized region. Regions modified from Wijk *et al.* (1959) and Good (1974).



Taxon	North America			Europe	Asia		
	Am. 1	Am. 2 (Gt Lakes)	Am. 2		As.1	As. 2	As. 3
L. mutabilis				■			
L. atricha	■						
L. incurvata var. *gigantea*	■						
L. saviana	■			■			
L. incurvata var. *tenuiretis*	■			■			
L .radicosa var. *denudata*	■			■			
L .radicosa var. *compacta*	■		■	■			
L. stenophylla	■		■	■			
L. saxicola	■		■	■	■	■	■
L. patens	■	■	■	■	■	■	
L. incurvata var. *incurvata*	■	■	■	■	■	■	■
L .radicosa var. *radicosa*	■	■	■	■	■	■	■

Figure 3.5. Global distribution of taxa in *Lescuraea*. Taxa occuring in a region are represented by bars. Generalized regions are Am. 1 - western North America; Am. 2 - eastern North America; As. 1 - north, central, & northeast Asia; As. 2 - East Asia; As. 3 - south-central Asia.

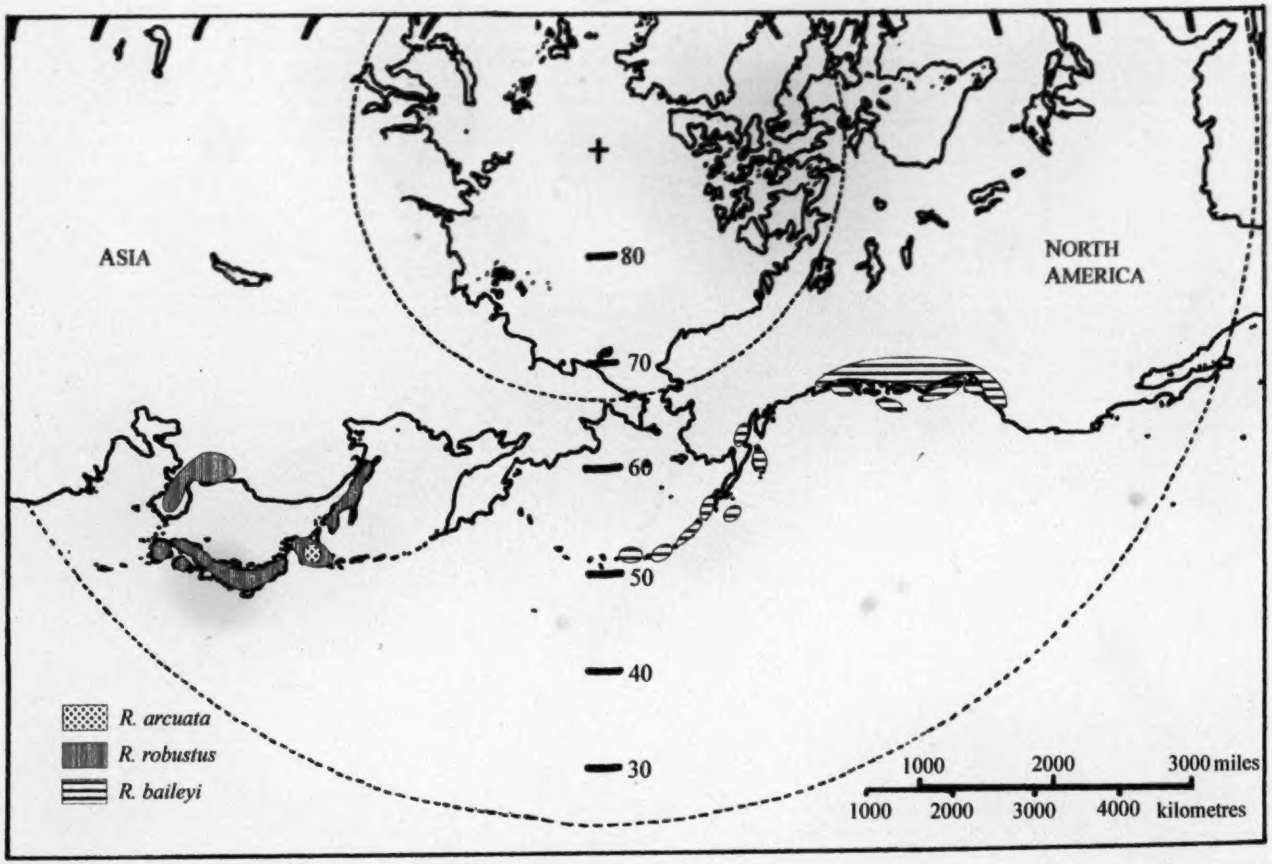

ASIA
NORTH AMERICA
80
70
60
50
40
30
R. arcuata
R. robustus
R. baileyi
1000
2000
3000 miles
1000
2000
3000
4000
kilometres

Figure 3.6. Amphi-Pacific distribution of *Rigodiadelphus*

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Chapter 4

CONCLUSION

Taxonomy, the science of naming, describing, identifying, and classifying organisms based on morphology (Bischler and Boisselier-Dubayle 1998) and other characters, is considered by some to be "the operational core of systematics (Novacek 1992)." Both work together to create order within nature, to determine the diversity and distribution of taxa, and to reflect patterns of relationships (Novacek 1992).

A taxonomic revision of *Lescuraea* Bruch & Schimp. *in* B.S.G. (including *Pseudoleskea* Bruch & Schimp. *in* B.S.G) reveals seven species in North America, with infraspecific variation resulting in six described varieties. Two taxa (*Lescuraea julacea* and *L. radicosa* var. *pallida*) have been placed in synonymy with other taxa in *Lescuraea*, one taxon (*L. arizonae*) has been reassigned to *Pseudoleskeella*, and a single species (*L. baileyi*) has been transferred to *Rigodiadelphus*. *Lescuraea radicosa* has been proposed as a conserved name with the acceptance of *Leskea brachyclados* as an earlier synonym. Examination of a number of species from around the world has resulted in their transfer from *Lescuraea* into entirely other families, with the exception of three sterile taxa that almost certainly belong in *Pseudoleskeella*. A revision of an additional 16 taxa would complete a monograph of *Lescuraea*.

Morphological characters particularly informative for the taxonomic revision were: stem transverse section; paraphyllia type and abundance; degree of recurvature and serrations of leaf margins; leaf cell and adaxial costal papillosity; inner perichaetial leaf stance, shape, and costal length; and characters associated with the peristome. With respect to the exostome the nature of the ornamentation of the OPL (e.g., striae vs. papillose-striae, and ridges) has been relatively overlooked in the past, but has been useful here. Buck and Crum (1990) recognised the Leskeaceae "primarily on the basis of gametophytic characters … and perceive[d] a habitat-driven, sporophyte reduction series." Similarly, sporophytes at different stages of reduction are evident in *Lescuraea*, and have been informative at the subgeneric level. An infrageneric classification of *Lescuraea* is proposed, with subgenera *Lescuraea* and *Pseudoleskea* accommodating one and six species respectively (of those I examined, primarily North American taxa).

In parallel to the completion of a future monograph, it would be worthwhile to establish a species phylogeny of all accepted taxa in *Lescuraea*. Hypotheses of infrageneric relationships and a detailed infrageneric classification can then be presented, thus supporting or providing insight into the proposed classification.

The phytogeographical distribution of *Lescuraea* is clearly Holarctic. However, a small Gondwanan element exists if examination of the seven African taxa supports their inclusion within *Lescuraea*. All taxa in *Lescuraea* inhabit montane to alpine slopes at elevations of 300 to 3350 metres, with the majority at elevations in excess of 1200 m. Taxa in both subgenera prefer a typical mountain climate of cooler and wetter conditions (Lisowski and Kornas 1966), and some are often found at high elevations near areas of melting snow (Lawton 1971). Habitat preferences of *Lescuraea* include upper montane forests to alpine tundra, where taxa are predominantly saxicolous or rarely corticolous in the former zone, and saxicolous or even terricolous in the latter zone. Substrate preferences for most taxa include siliceous rocks (igneous, gneiss, quartzite), with some taxa collected from calcareous rocks or twigs and branches.

The centres of diversity for *Lescuraea* appear to be in North America and in Europe. In addition, two taxa are endemic to North America, while a single taxon is endemic to Europe. However, a discussion concerning the centre of diversity invariably raises questions about the evolution of *Lescuraea*.

Lescuraea may have evolved relatively recently in Europe in the Middle Eocene (50 myr BP) to the Early Miocene (23.7 myr BP), dispersing to North America and to Asia. This hypothesis is based on historical evidence of plate tectonics; fossilized remains of pleurocarpous mosses from Miocene (25-13 myr BP) deposits in Poland (Jovet-Ast 1967); and evidence of rapid diversification of other mosses during angiosperm radiation in the Early Tertiary (64-40 myr BP). Unfortunately, without a fossil record or species phylogeny, the evolution of *Lescuraea* remains open to debate. Schofield (1968, 1969, 1976, 1980) examined the phytogeography of mosses including *Lescuraea*, focusing mostly on North America and British Columbia. Schofield (1980) hypothesized that bryophytes display a vicarious distribution, showing the same kinds of disjunct patterns as angiosperms (Crum 1972, Schofield and Crum 1972). Consequently, this has lead some researchers to conclude that bryophytes are not subject to long-distance dispersal, despite their small diaspores. Since all taxa in *Lescuraea* are dioicous and only infrequently produce sporophytes, selection pressures could restrict their current range to moist and cool, montane to alpine slopes of Holarctic mountain ranges, where in the past they may have displayed a more continuous circumboreal distribution. As a result, taxa in *Lescuraea* may have held out in microhabitats as relict populations during major climatic changes, and then expanded their ranges again afterwards.

Currently, there are no conclusive answers to the origins and causes of the proposed endemics and disjuncts of *Lescuraea*, although the hypothesis that *Lescuraea* displays a vicarious distribution appears well supported. An understanding of the taxa, including their biogeographical and historical distributions, is essential to discussions of conservation priorities (Stiassny 1992). With global warming and depletion of the ozone layer a reality, plants that have adapted to moist and cool habitats at higher elevations may be in imminent danger of extinction. As the global temperature rises, taxa that favour or compete well at lower elevations, may find suitable habitats at higher elevations, thus constricting or eliminating the range of native taxa. Therefore, it is important that the habitats and taxa of *Lescuraea* be monitored, not only for the intrinsic value of this bryophyte genus, but also for the protection of the entire subalpine and fragile alpine ecosystem.

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